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I. Populations in Natural Habitats

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Small Mammal Populations of Nortneastern Alberta
I. Populations in Natural Habitats

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The Hon. J.W. (Jack) Cookson
Minister of the Environment
222 Legislative Building
Edmonton, Alberta

Sir:

Enclosed is the report "Small Mammal Populations of Northeastern Alberta I. Populations in Natural Habitats".

This report was prepared for the Alberta Oil Sands Environmental Research Program, through its Land System, under the Canada-Alberta Agreement of February 1975 (amended September 1977).

Respectfully,

W. Solodzuk, P.Eng.
Chairman, Steering Committee, AOSERP
Deputy Minister, Alberta Environment

SMALL MAMMAL POPULATIONS OF NORTHEASTERN ALBERTA
I. POPULATIONS IN NATURAL HABITATS

by

JEFFREY E. GREEN

LGL Limited
environmental research associates

for

ALBERTA OIL SANDS ENVIRONMENTAL
RESEARCH PROGRAM

LS 7.1.2

November 1980

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ABSTRACT

A study of small mammal populations (small rodents and snowshoe hares), habitat use, small rodent diets, and small mammal damage in natural forest and successional communities was begun in June 1978 and continued until November 1979. Based on population sizes and distributions, four species of small mammals, *Clethrionomys gapperi, Microtus pennsylvanicus, Peromyscus maniculatus,* and *Lepus americanus,* were determined to be important components of the boreal forest ecosystem in northeastern Alberta. Twelve additional species of small mammals were captured during this program but numbers were small.

Indices of habitat quality based on peak population sizes, responses to habitat structure, habitat preferences, an index of dispersal, reproductive activity, and nutritional condition indicated that balsam poplar forests and young successional areas were high quality habitats for most small rodents, whereas black spruce and tamarack forests were marginal. In contrast, black spruce communities were near-optimal habitats for *L. americanus*, and balsam poplar forests were only moderately well-suited.

Feeding habits of *C. gapperi, M. pennsylvanicus*, and *P. maniculatus* in this study were similar to diets described previously in other studies. Lichens, *Carex* spp., and arthropods were the major foods for each species, respectively. Mycorrhiza were consumed regularly by all species. Bark tissue of trees and shrubs was found most frequently in *C. gapperi* diets, but was limited in diets of *M. pennsylvanicus*. Consumption of bark by *P. maniculatus*, previously unreported in the literature, was common during the spring and fall.

Damage to trees and shrubs in natural and successional areas by small rodents was limited. In contrast, browsing by snowshoe hares was high in some communities, notably tamarack forests. Some species of trees and shrubs were highly susceptible to damage, whereas others were resistant. Some factors associated with local variation in amounts of small mammal damage are discussed.

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1. INTRODUCTION

The activities associated with oil extraction developments in the Athabasca Oil Sands of northern Alberta will affect the natural environment. In an effort to assess the impact of these developments on the floral and faunal communities of the Athabasca Oil Sands area, the Alberta Oil Sands Environmental Research Program (AOSERP) is conducting baseline environmental studies in the vicinity of the Athabasca Oil Sands deposits [hereafter called the AOSERP study area (Figure 1)].

Although the direct impacts of oil sands developments on small mammal populations will likely be considered an unimportant component in the overall assessment of impacts on wildlife and vegetation, disruption of small mammal populations by oil sands developments could result in changes in the abundance of prey for furbearers and raptors, in rates of mineral transport and soil development, in soil drainage, in seed dispersal, in vegetation composition and productivity, and in insect numbers (DeCapita and Bookout 1975; Golley et al. 1975; Goszczynska and Goszczynski 1977; Grant and French 1980). These changes may intensify the effects of oil sands development on other key wildlife species. Information on at least the most abundant species of small mammals present in the AOSERP study area consequently should be included in the assessment of environmental impacts of oil sands development and in the formulation of mitigative measures.

The main purpose of this study was to collect detailed baseline information on populations and habitat use by small mammals. The specific objectives of the program (as described in the terms of reference) were to:

1. Determine the distribution and population densities of major small mammal species (small rodents and snowshoe hares) in the AOSERP study area;
2. Assess demographic trends (changes in population size, reproduction, population losses, etc.) of the major species of small mammals occurring in six of the major

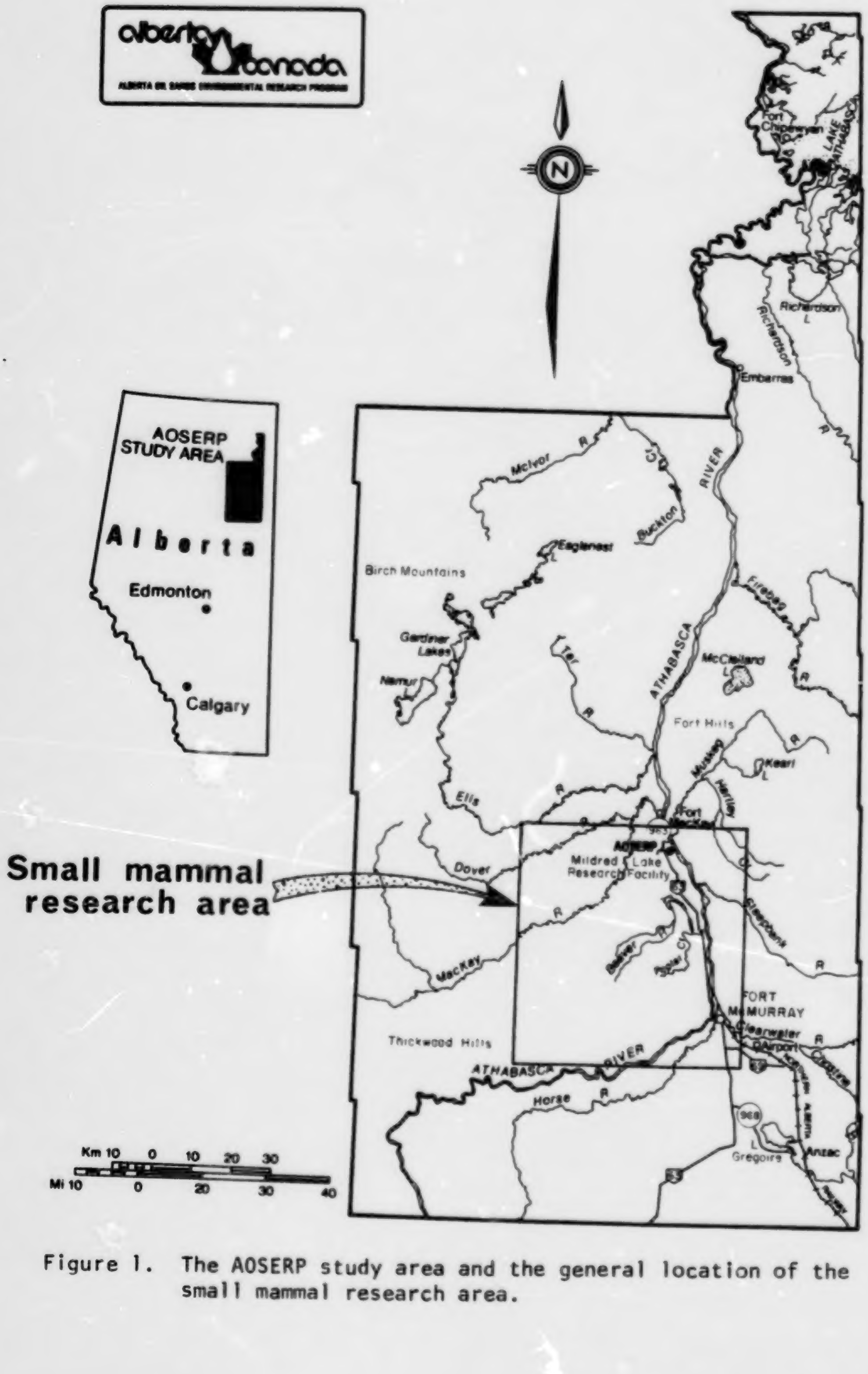
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Figure 1. The AOSERP study area and the general location of the small mammal research area.

habitat types of the AOSERP study area [as described by Stringer (1976)];

3. Evaluate habitat utilization and requirements of the major species of small mammals in the AOSERP study area;
4. Determine the feeding habits of the major species of small rodents, based on analyses of stomach contents; and
5. Determine the levels of damage by small mammals to woody-stemmed plants in natural habitats and in naturally revegetating areas (to complement similar surveys on reclamation areas).

These objectives were to be fulfilled by a four-year study of small mammal populations and habitat use, and by a review of the literature pertaining to the distribution, habitat utilization, and demography of the major species of small mammals in the AOSERP study area. The literature review has been completed (Green 1979a). However, as a result of changes in program funding, the present report only represents the final assessment of baseline information collected during field studies conducted from June 1978 to January 1980. A holistic evaluation of the direct and indirect environmental impacts of oil sands development is to be conducted at a later date in the AOSER Program.

Because it was not feasible to study small mammal populations throughout the AOSERP study area, small mammal communities within representative habitat types were studied intensively. Knowledge of the baseline states of these communities may be extrapolated to other areas and is needed to adequately assess and mitigate the impacts of oil sands development on the small mammal community. Caution must be applied in such extrapolations, however, because several species of small mammals present in the AOSERP study area undergo large changes in abundance--*Clethrionomys gapperi* and *Microtus pennsylvanicus* populations exhibit regular fluctuations every 3 to 5 years (Krebs and Myers 1974), whereas *Lepus americanus* populations undergo regular 8 to 11 year cycles of abundance (Keith and Windberg 1978). Because habitat use can change during these cyclic fluctuations (Grant 1970, 1971a; Keith and Surrendi 1971), characteristics of a population within one habitat in one year will not necessarily approximate characteristics of other populations in similar habitats during different phases of these population fluctuations.

The results of this study have been divided into five sections: small rodent demography; small rodent habitat use; small rodent dietary analyses; snowshoe hare demography and habitat use; and damage by small mammals to woody-stemmed plants. Each section includes a description of specific methods, analyses, and a discussion of the results. The five sections are preceded by a description of the study area and are followed by a study synthesis.

The term 'small mammals' will be used to describe collectively all species of cricetids (mice and voles), sciurids (chipmunks, red squirrels, and flying squirrels), and leporids (hares and rabbits). The term 'small rodents' will be used only in reference to cricetids. Mammalian nomenclature follows that of Banfield (1977). Plant nomenclature follows that of Moss (1967). Common names and scientific equivalents of plants discussed in this report are provided in Appendix 11.1 (Table 41).

2. GENERAL METHODS

Information on the distributions, abundances, and habitat preferences of the major small rodent species of the AOSERP study area was obtained from eight different study areas. One small rodent study area was established in each of six different natural habitats and in each of two disturbed but naturally revegetating areas. Data were also obtained on the levels of small mammal damage to trees and shrubs in each of these eight study areas. Information on the distribution, abundance, and habitat preferences of snowshoe hares was obtained from four study areas located in four different natural habitats.

2.1 NATURAL HABITATS

In mid-June 1978, small mammal study plots were established in six of the 10 major vegetation types of the AOSERP study area [as described by Stringer (1976)]; study plots were not established in the other four vegetation types because they were believed to be unsuitable habitats for small mammals. Plots were located in white spruce-aspen forest (referred to as the Aspen study area) (Figure 2), jack pine forest (Jack Pine study area), tall willow communities (Willow study area), bottom-land balsam poplar forest (Balsam Poplar study area), black spruce bog forest (Black Spruce study area), and semi-open black spruce-tamarack bog forest (Tamarack study area). Snowshoe hare study plots were established in jack pine forest (referred to as the SH-Jack Pine study area), white spruce-aspen forest (SH-Aspen study area), bottom-land balsam poplar forest (SH-Balsam Poplar study area), and black spruce bog forest (SH-Black Spruce study area).

The Aspen and SH-Aspen study areas were located in an upland white spruce-aspen forest type. The stand was composed of aspens (*Populus tremuloides*), 10 to 12 m high, and some white spruce (*Picea glauca*), with a well-developed stratum of medium and low shrubs (0.5 to 1.0 m in height) dominated by *Amelanchier*

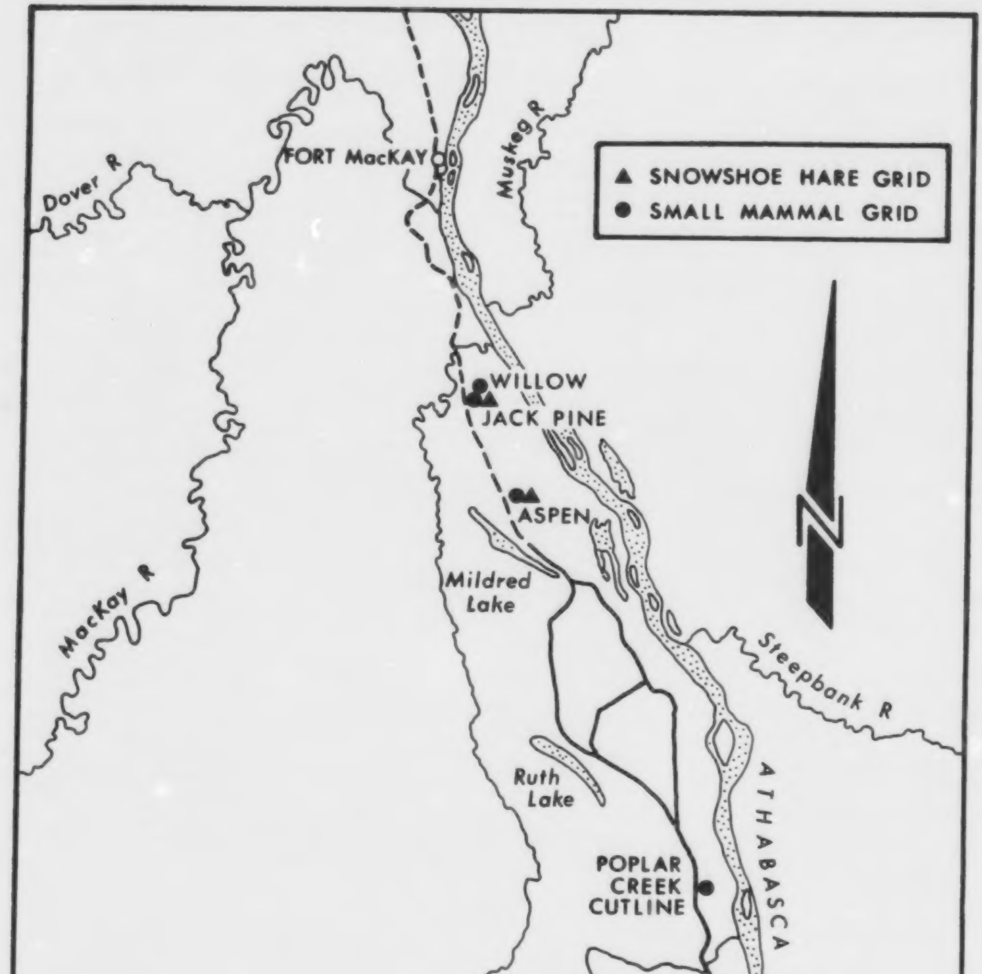
▲ SNOWSHOE HARE GRID
● SMALL MAMMAL GRID
FORT MacKAY
Dover R
Muskeg R
WILLOW
JACK PINE
ASPEN
Mildred Lake
MacKay R
Steepbank R
Ruth Lake
POPLAR CREEK CUTLINE
ATHABASCA RIVER
63
Beaver Ck
Poplar Ck
BALSAM POPLAR
THICKWOOD HILLS
TAMARACK
THICKWOOD CUTLINE
BLACK SPRUCE
FORT McMURRAY
N
0 2 4 6 8 10
Miles
Kilometres
0 2 4 6 8 10 12 14 16

Figure 2. Locations of the eight small mammal study plots and the four snowshoe hare study plots.

alnifolia, Rosa spp., *Symphoricarpos albus, Viburnum edule,* and *Vaccinium myrtilloides.*

The Jack Pine and SH-Jack Pine study areas were located mainly in a jack pine forest on well-drained, sandy soil. Jack pines (*Pinus banksiana*), 12 to 15 m in height, were the major tree species although a large number of aspen saplings (1 to 3 m in height) were also present. The understory was characterized by extensive areas of fruticose lichens (*Cladina* spp. and *Cladonia* spp.) interspersed with areas of green alder (*Alnus crispa*) and a sparse dwarf shrub stratum of *Arctostaphylos uva-ursi* and *Vaccinium caespitosum.* Approximately half of the SH-Jack Pine and several small areas of the Jack Pine study areas were situated in low, moist areas dominated by tall willow (*Salix* spp.) scrub.

The Willow study area was situated in an area of damp soil and was dominated by dwarf birch (*Betula glandulosa*) and willows (*Salix* spp.) that varied from 0.5 to 3 m in height. The understory was composed primarily of *Vaccinium uliginosum* and a dense mat of sedges.

The Balsam Poplar and SH-Balsam Poplar study areas were located in a mature stand of balsam poplars (*Populus balsamifera*) from 25 to 30 m high. The understory was composed primarily of a 3 to 5 m canopy of alders (*Alnus* spp.) interspersed with clumps of a lower shrub stratum (1 to 2 m high) dominated by *V. edule, Ribes oxyacanthoides, Ribes triste, Rubus melanolasius* and *Rosa* spp.

The Black Spruce and SH-Black Spruce study areas were established in a black spruce (*Picea mariana*) forest of low to medium density. Most trees were only 4 to 6 m high. A few tamarack (*Larix laricina*) and some paper birch (*Betula papyrifera*) were also present. The understory was composed primarily of *Ledum groenlandicum* and *V. myrtilloides* although *Salix* spp. and *B. glandulosa* occurred on some parts of the snowshoe hare and small rodent study areas. Sphagnum mosses were the major ground cover.

The Tamarack study area was located in a poorly drained area dominated by a sparse cover of black spruce and tamarack. Shallow pools of water (2 to 30 cm in depth) were present on some parts of the study area throughout the spring, summer, and fall. Few trees exceeded heights of 6 to 8 m. The shrub understory was composed primarily of *B. glandulosa* and *Salix* spp. The ground cover consisted of an almost continuous layer of sphagnum mosses with a dwarf shrub layer composed largely of *L. groenlandicum*, *Vaccinium vitis-idaea*, and *Rubus chamaemorus*.

2.2. NATURALLY REVEGETATING AREAS

Two small rodent plots were established in recently disturbed but naturally revegetating areas. Although naturally disturbed areas (i.e., recently burned) would have been preferable sites, no sufficiently large burned areas were accessible. Two cutline right-of-ways were chosen instead.

The Poplar Creek Cutline study area was established on a section of the Alberta Power Limited right-of-way, 22 to 23 July 1978 (Figure 2). The area was cleared and burned in 1972 and has received no further treatment since that time (letter dated 1 September 1978, L. McRae, Alberta Power Ltd.). The cutline was bounded on the north and south edges by aspen forest. Vegetation on the cutline was characterized by a sparse regrowth of *Salix* spp., *Rosa* spp., *Rubus melanolasius*, *Lonicera* spp., and *R. oxyacanthoides* with a dense ground cover of grasses and sedges.

The Thickwood cutline study area was established during 20 to 21 June 1978 on a portion of the pipeline right-of-way belonging to Simmons Pipeline Limited. The right-of-way was cleared in late November and December 1976 (letter dated 9 January 1979, L.T. Pasiechnyk, Project Engineer, Simmons Pipeline Ltd.). Brush was bulldozed, wind-rowed, and burned. The area has received no further treatment to date. Very little vegetative cover was present on this area in June 1978. The sparse ground cover consisted primarily of very young *P. tremuloides*, *P. balsamifera*, *Rosa* spp., *Equisetum* spp., and some grasses. Forest habitats, adjacent to this study area, were primarily dense, mature stands of *P. tremuloides* and *A. balsamea*.

2.3 SNAP-TRAP CENSUS AREAS

Snap-trap censuses of small rodents were undertaken to provide information on the abundance, distribution, habitat preferences and reproductive indices of the major small rodent species from a wider geographic area than that sampled by live-trapping. In 1978 and 1979, snap-trap censuses were conducted in natural areas adjacent to Highway 63 (and its extension past Fort MacKay) and the road to the Thickwood Fire Tower (Figure 3). In 1978, 19 snap-trap lines were also set in remote areas (in the vicinities of the Birch Mountain Fire Tower, the Muskeg Mountain Fire Tower, and the Richardson sand dunes). Results from the 19 snap-trap censuses in these remote areas are discussed by Green (1979b).

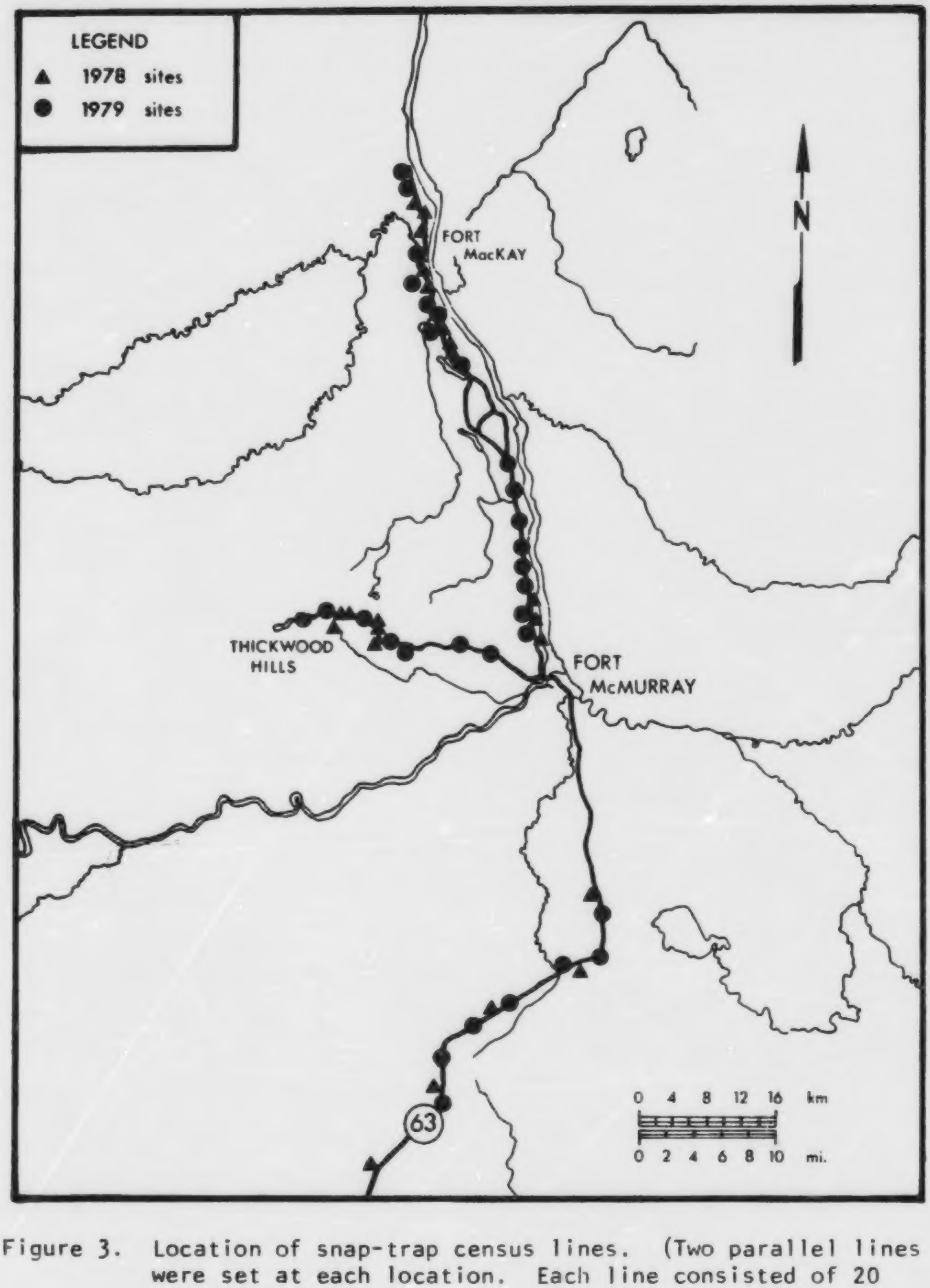
LEGEND
▲ 1978 sites
● 1979 sites
N
FORT MacKAY
THICKWOOD HILLS
FORT McMURRAY
63
0 4 8 12 16 km
0 2 4 6 8 10 mi.

Figure 3. Location of snap-trap census lines. (Two parallel lines were set at each location. Each line consisted of 20 trap stations with three traps at each station.)

3. SMALL RODENTS: DEMOGRAPHY

Species of small rodents inhabiting the boreal forest show distinct preferences for specific habitats (Green 1979a). Selection of these habitats reflect responses to environmental and physiological variables, the overall effects of which are related directly to natural selection; individuals that utilize habitats in which large numbers of offspring can be successfully raised will be selected over individuals that chose marginal habitats where reproductive success is low (Krebs 1978). The 'quality' of a habitat for each species of small rodent consequently should be reflected by the characteristics of the local population, particularly those characteristics related to reproductive success.

Assuming that habitat selection is related to reproductive success, populations in better quality habitats should be characterized by large population numbers, good survival, high recruitment, high reproductive success (e.g., longer breeding season, high breeding activity, high pregnancy rates), and good nutritional condition [see Krebs and Myers (1974) for a review]. Balanced sex ratios, moderate to high rates of immigration, and limited emigration (except perhaps during peak population densities) also may be indicative of populations in optimal habitats.

Demographic information for small rodent populations in the AOSERP study area, obtained during a two-year program of live-trapping and snap-trapping in specific habitat types, was used primarily to evaluate changes in population size and to provide additional information on habitat quality and use.

3.1 METHODS

3.1.1 Live-trapping Techniques

Small rodent live-trapping techniques were similar to those described by Krebs et al. (1969). The six small rodent trapping grids in natural habitats were each 0.81 ha in size and consisted of a 10 x 10 grid of trapping stations at 10 m intervals. The two cutline grids were 0.76 ha in size and each consisted of a 5 x 20 grid of trapping stations at 10 m intervals. One Longworth Trap was placed within a 1.5 m radius of each trap station. Traps were prebaited (trap doors were locked open) for 2 wk before commencing live-trapping. Cotton felt for bedding and oat groats for bait were placed in the nest box of each trap and were replenished when necessary. Between trapping periods, the doors on all traps were locked open.

Fifteen chipmunk/squirrel traps (Tomahawk #201) were also placed on each small rodent trapping grid. One trap was set at the first, fifth, and tenth trap station on alternate rows of the trapping grid. Traps were not prebaited but were baited with peanut butter on the first day and were rebaited as necessary.

Each trapping period consisted of 3 d of live-trapping. All traps were set during the afternoon of the first day. All traps were checked and reset the following morning and again in the afternoon. On the morning of the third day, all traps were checked and locked open until the next trapping period.

When first captured, all small rodents were ear-tagged with a numbered fingerling fish tag. Following tagging or when tagged animals were captured during subsequent trapping periods, the tag number, species, trap location, sex, breeding condition, weight, number of wounds on the posterior portion of the body, the number of subdermal parasites (*Cuterebra* spp.), and the number of attached ticks were recorded.

In 1978, most small rodent trapping areas were trapped at 2 wk intervals from 30 June to 16 November; biweekly trapping on the Poplar Creek cutline grid commenced 2 August and continued until 10 November. In 1979, all small rodent trapping areas were trapped at 3 wk intervals from 13 May to 11 November.

3.1.2 Snap-trapping Techniques

Snap-trap censuses of small rodents were conducted according to techniques outlined for the North American Census of Small Mammals program (Calhoun and Casby 1958). Snap-trap lines consisted of 20 stations spaced at 15 m intervals along a straight line. Three Woodstream Museum Special Snap Traps were set within 2 m of each station and were baited with peanut butter. Traps were set in the afternoon of the first day and were checked daily for 3 d. Two parallel lines placed approximately 100 m apart were set at each sampling location. In 1978, six snap-trap lines usually were set every 3 wk from the 17 July to 17 October. In 1979, eight snap-trap lines were set every three weeks from 10 May to 3 November.

All animals captured in snap-traps were autopsied to provide information on reproductive characteristics and nutritional condition. For each animal autopsied, the body weight, total length, tail length, skull (zygomatic) breadth, reproductive condition, number of subdermal parasites (*Cuterebra* spp.), and a qualitative index of the amount of fat in the abdominal mesentery [no fat (1) to very fat (5)] were recorded (Krebs 1964). Tissue samples were retained for toxicological examination (pers. comm., B. Munson, Research Management Division, Alberta Environment) and are presently deposited at the Alberta Environmental Centre, Vegreville, Alberta.

3.1.3 Data Analyses

Small mammal live-trapping and snap-trapping data were analyzed using computer programs provided by C.J. Krebs of the University of British Columbia. Additional programs for specific analyses of population data were developed as needed. Original data and programs are stored at the University of Alberta Computing Centre and may be accessed with permission of the author.

3.2 POPULATION CHANGES

Fourteen species of small mammals were captured in 1978 and 1979 during the course of the live-trapping and snap-trapping program of small rodents in the AOSERP study area. Of these 14 species, only *Clethrionomys gapperi*, *Microtus pennsylvanicus*, and *Peromyscus maniculatus* were captured in sufficient numbers to merit detailed analyses. Other small mammal species captured were *Microsorex hoyi, Sorex cinereus, Sorex obscurus, Sorex arcticus, Phenacomys intermedius, Synaptomys borealis, Zapus hudsonicus, Eutamias minimus, Tamiasciurus hudsonicus, Glaucomys sabrinus, Mustela nivalis,* and *Mustela erminea*--because of small sample sizes (Table 1), analyses for these 11 species were limited.

3.2.1 Changes in Abundance

3.2.1.1 Live-trapping areas. Densities of small rodent populations usually have been assessed using mark-recapture methods of estimating population size. To avoid the assumptions of mark-recapture techniques (Roff 1973), a complete enumeration of small mammal populations within each live-trapping area was attempted. The minimum number known to be alive (MNA) (Chitty and Phipps 1966) during each biweekly sampling period was used as a biased estimate of the trappable population size.

Biases in population estimates (usually underestimates) may be caused by poor trappability, poor trap availability, or social interactions (Boonstra and Krebs 1978). An attempt was made to minimize the biases inherent in small mammal trapping studies by (1) ensuring that each trapping area was saturated with traps (i.e., by using a small inter-trap distance), and (2) by only using MNA estimates when trappability exceeded 50% (Hilborn et al. 1976).

Estimates of trappability were calculated to provide an indication of the reliability of the calculated MNA. Minimum unweighted trappability was calculated for a population of N captured individuals according to the following formula (Boonstra and Krebs 1978):

$$\text{Minimum Unweighted Trappability} = \frac{1}{N} \sum_{i=1}^{N} \frac{\text{number of trapping periods during which an animal was captured}}{\text{number of possible trapping periods for that animal}}$$

The first and last capture of each individual are not included in these calculations (because all animals are necessarily caught at these times).

Table 1. Total numbers of live captures of less commonly captured species of small mammals.

Live-trapping Area	Year	Total Number of Captures *S. cinereus*/ *M. hoyi*[a]	*S. obscurus*/ *S. arcticus*[b]	*S. borealis*	*Z. hudsonicus*	*E. minimus*	*T. hudsonicus*	*G. sabrinus*	*M. nivalis*	*M. erminea*
Aspen	1978	22	2	0	2	20	24	5	0	4
	1979	17	0	0	1	19	21	0	0	1
Jack pine	1978	6	0	0	0	18	8	6	0	0
	1979	7	0	0	0	7	0	0	0	0
Willow	1978	46	5	1	0	4	9	0	0	2
	1979	23	0	3	0	0	0	0	0	0
Balsam poplar	1978	15	1	0	0	15	0	0	0	2
	1979	5	2	0	0	13	1	0	0	2
Poplar Creek cutline	1978	2	9	0	3	3	1	0	0	2
	1979	0	19	0	3	0	3	0	0	10
Black spruce	1978	4	0	0	2	0	0	0	0	2
	1979	9	1	0	0	0	2	0	0	0
Thickwood cutline	1978	0	0	0	0	9	0	0	0	0
	1979	2	0	0	0	3	0	0	0	2
Tamarack	1978	4	4	0	0	8	0	0	0	0
	1979	11	3	0	0	0	0	0	1	2

[a] Because *M. hoyi* and *S. cinereus* could not be differentiated reliably on the basis of external characteristics, they consequently have been grouped together.

[b] Because *S. obscurus* and *S. arcticus* could not be differentiated reliably on the basis of external characteristics they consequently have been grouped together.

Estimates of minimum unweighted trappability were calculated for *C. gapperi, M. pennsylvanicus,* and *P. maniculatus* for both the summer and fall periods (Table 2). Trappability estimates for most species exceeded 50% and the MNA consequently should underestimate the trappable population sizes by acceptably small amounts. However, trappabilities for *C. gapperi* on the Thickwood cutline grid in the summer of 1979, for *M. pennsylvanicus* on the Aspen and Balsam poplar grids in the fall of 1978 and on the Balsam Poplar, Black spruce, Thickwood cutline, and Tamarack grids in the fall of 1979, and for *P. maniculatus* on the Aspen and Balsam poplar grids in the fall of 1978 were below 50%--in these cases, the MNA will be considered an underestimate of the trappable population size.

Comparisons of MNA estimates of *C. gapperi, M. pennsylvanicus,* and *P. maniculatus* populations on each of the eight study plots (Figures 4 to 11) indicated that habitat use, longer term population trends, and seasonal population fluctuations differed among areas.

Clethrionomys gapperi was the most abundant species on the Aspen and Jack Pine study areas; it was also one of the two most abundant species on the Balsam Poplar, Black Spruce, and Tamarack study areas. Generally, most *C. gapperi* populations declined between 1978 and 1979. However, the *C. gapperi* population on the Jack Pine study area was similar between years. In 1978, most *C. gapperi* populations reached peak population sizes in September and October but, in 1979, peak population sizes generally were reached by late September. In both years, most *C. gapperi* populations increased rapidly in early July and late August.

Microtus pennsylvanicus was the most abundant species on the Willow, Poplar Creek Cutline, and Thickwood Cutline study areas; it was also abundant on the Black Spruce and Tamarack study areas. Population sizes declined sharply in most habitats between 1978 and 1979. In 1978, most *M. pennsylvanicus* populations reached peak numbers by late August to early September. In 1979, the Thickwood Cutline and tamarack populations declined steadily throughout the

Table 2. Seasonal estimates of minimum unweighted trappability (MUT). (Calendar equivalents of the summer and fall periods in each year were: 1978--1 July to 25 September and 26 September to 9 November ; 1979--24 June to 20 September and 20 September to 9 November. N is the number of animals captured in three or more trapping periods.)

Grid	Species	1978				1979			
		Summer		Fall		Summer		Fall	
		MUT	N	MUT	N	MUT	N	MUT	N
Aspen	*C. gapperi*	77.6	42	92.3	52	72.5	20	50.9	19
	M. pennsylvanicus	59.4	8	6.7	5	50.0	2	-	0
	P. maniculatus	63.1	21	49.0	17	74.1	9	100.0	3
Jack pine	*C. gapperi*	77.4	19	89.4	22	92.9	14	53.0	17
	M. pennsylvanicus	82.1	14	100.7	7	-	0	-	0
	P. maniculatus	58.3	7	58.3	4	-	0	-	0
Willow	*C. gapperi*	86.6	18	94.7	25	64.3	7	77.9	12
	M. pennsylvanicus	63.3	60	71.5	45	78.6	14	57.8	15
	P. maniculatus	-	0	-	0	-	0	-	0
Balsam poplar	*C. gapperi*	76.8	96	81.0	78	80.3	32	66.7	20
	M. pennsylvanicus	68.1	6	25.0	4	81.3	8	27.8	6
	P. maniculatus	68.9	41	44.4	21	87.9	32	66.7	18
Poplar Creek cutline	*C. gapperi*	73.7	45	91.7	24	100.0	3	66.7	3
	M. pennsylvanicus	67.3	83	59.5	81	61.9	14	66.7	6
	P. maniculatus	61.5	13	80.8	13	53.3	5	-	0
Black spruce	*C. gapperi*	78.8	34	92.9	33	84.6	13	54.2	8
	M. pennsylvanicus	69.0	55	81.0	29	66.7	3	0.0	1
	P. maniculatus	66.7	4	100.0	4	62.5	4	-	0
Thickwood cutline	*C. gapperi*	65.3	18	75.6	15	40.8	8	100.0	1
	M. pennsylvanicus	75.4	60	76.5	44	70.0	16	0.0	1
	P. maniculatus	76.6	34	87.7	27	81.5	20	66.7	9
Tamarack	*C. gapperi*	74.1	51	86.2	59	81.7	10	51.9	9
	M. pennsylvanicus	76.1	60	78.8	44	50.0	15	33.3	7
	P. maniculatus	-	0	-	0	-	0	-	0

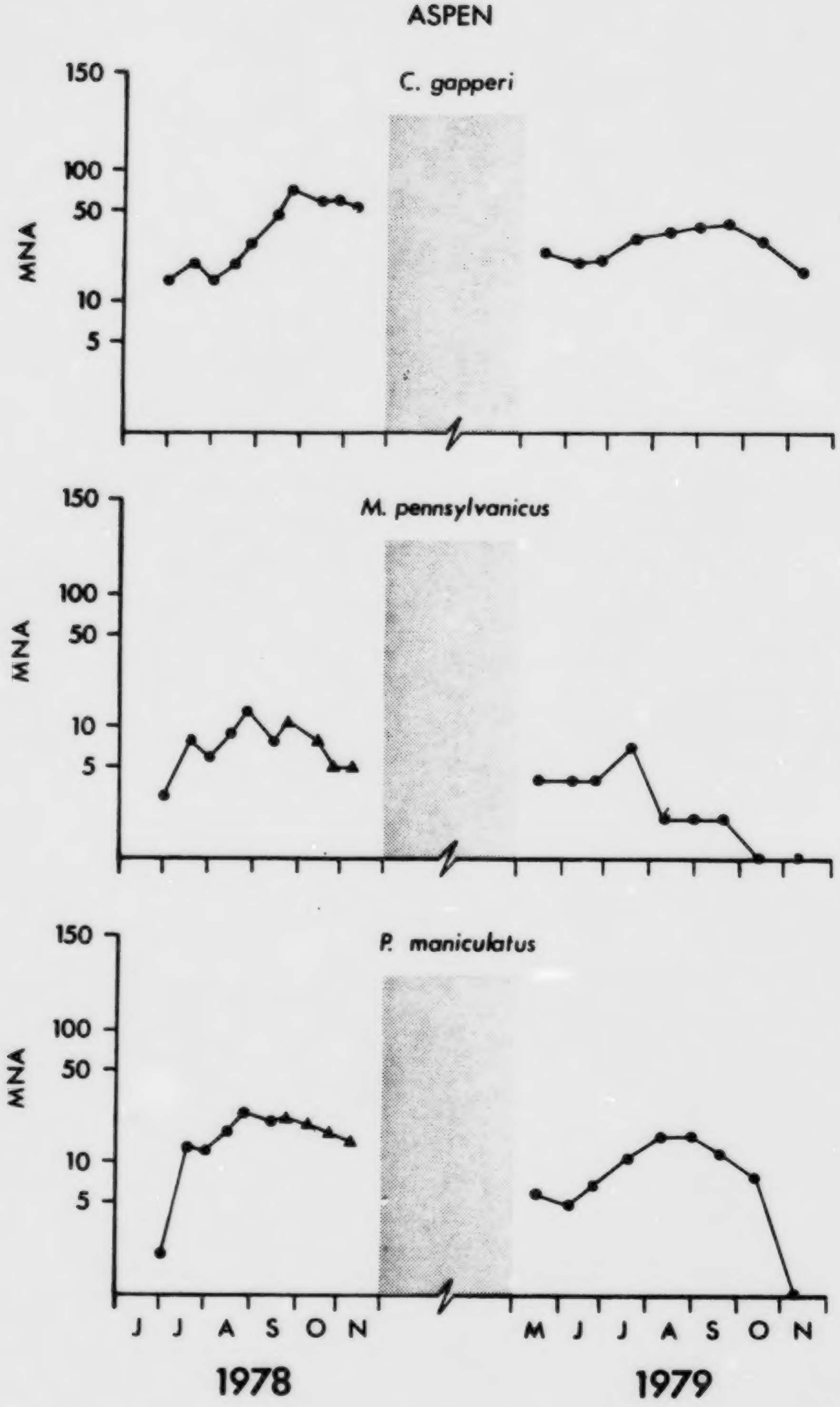

Figure 4. The MNA of small rodents on the Aspen study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

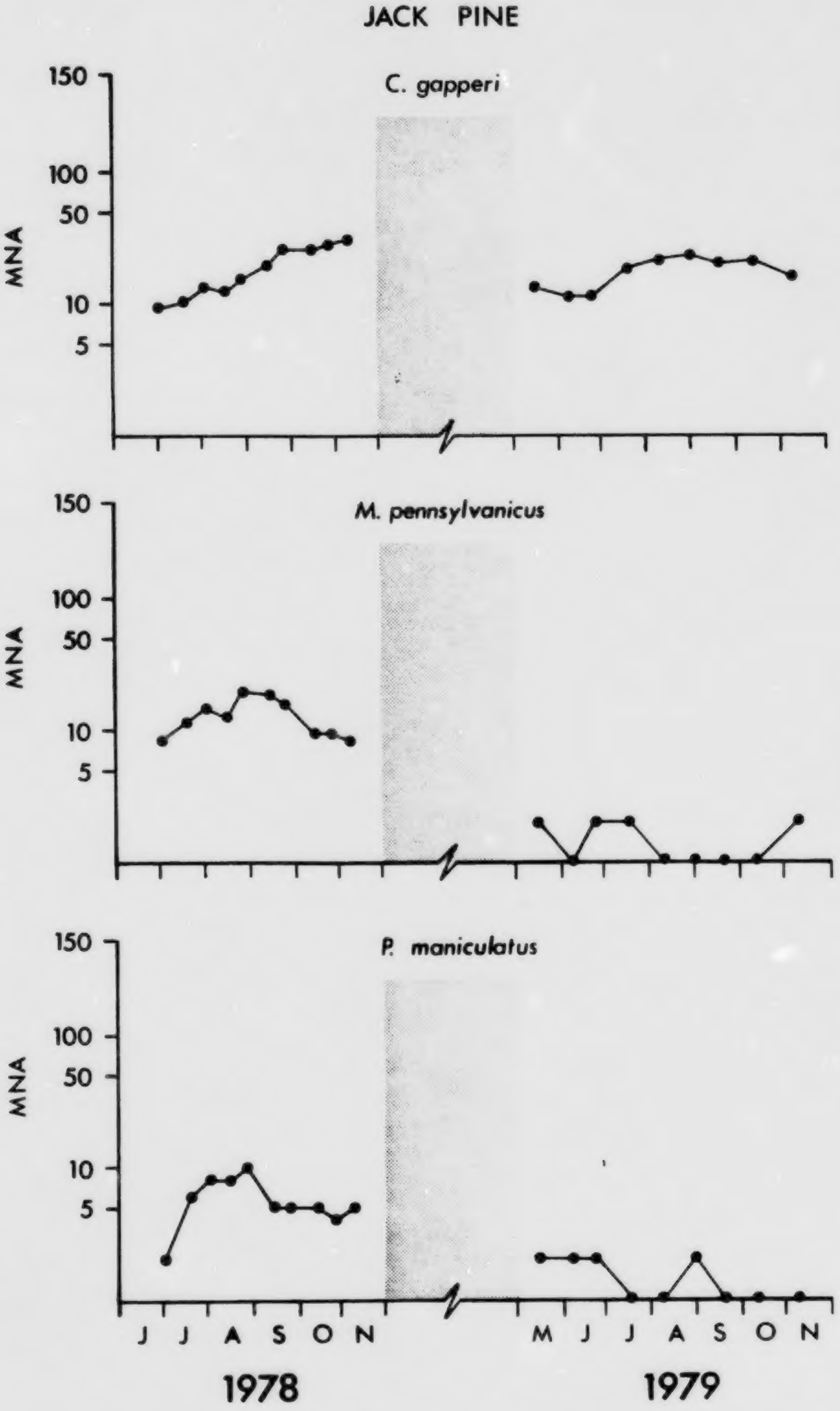

Figure 5. The MNA of small rodents on the Jack Pine study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

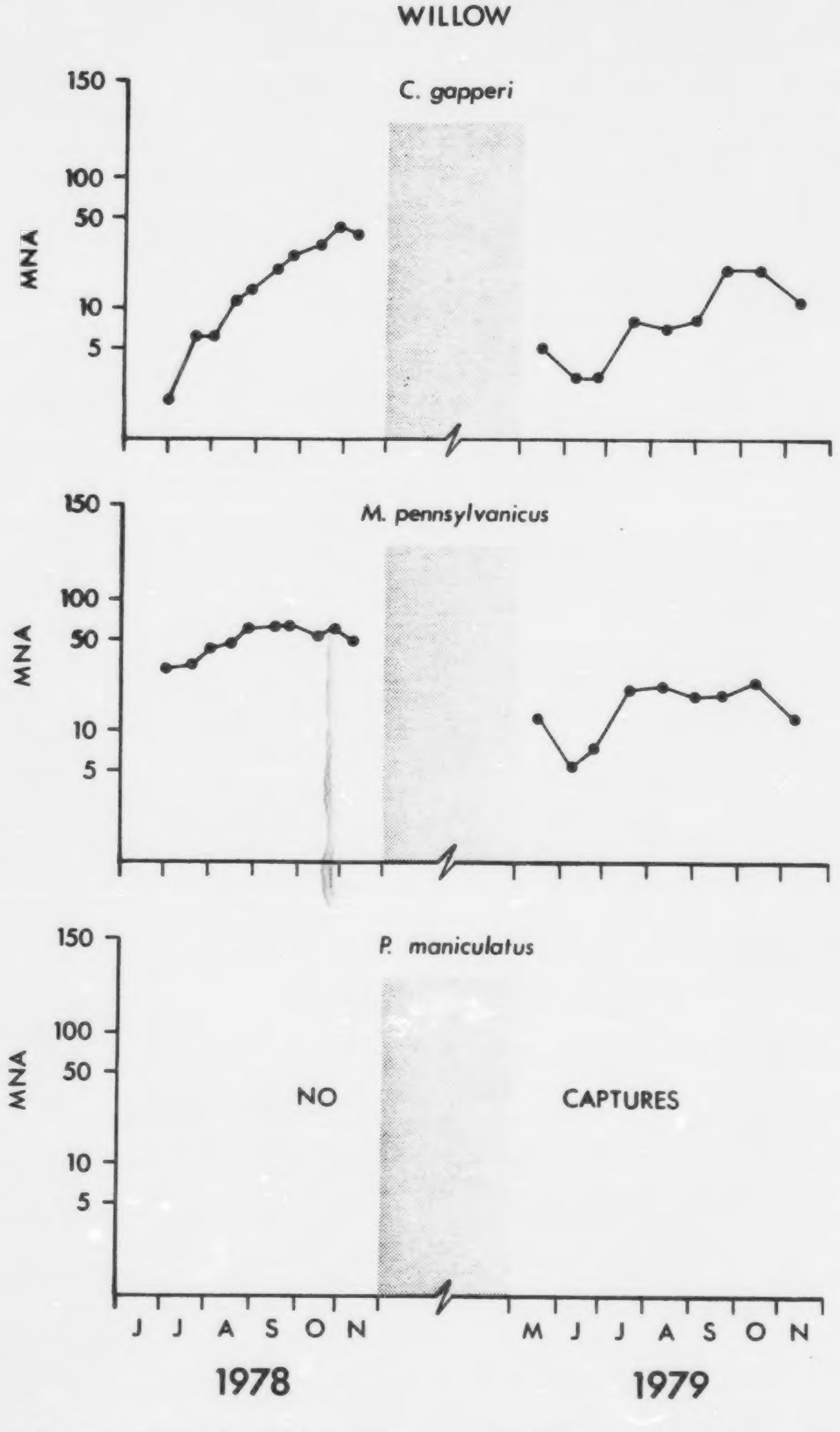

Figure 6. The MNA of small rodents on the Willow study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

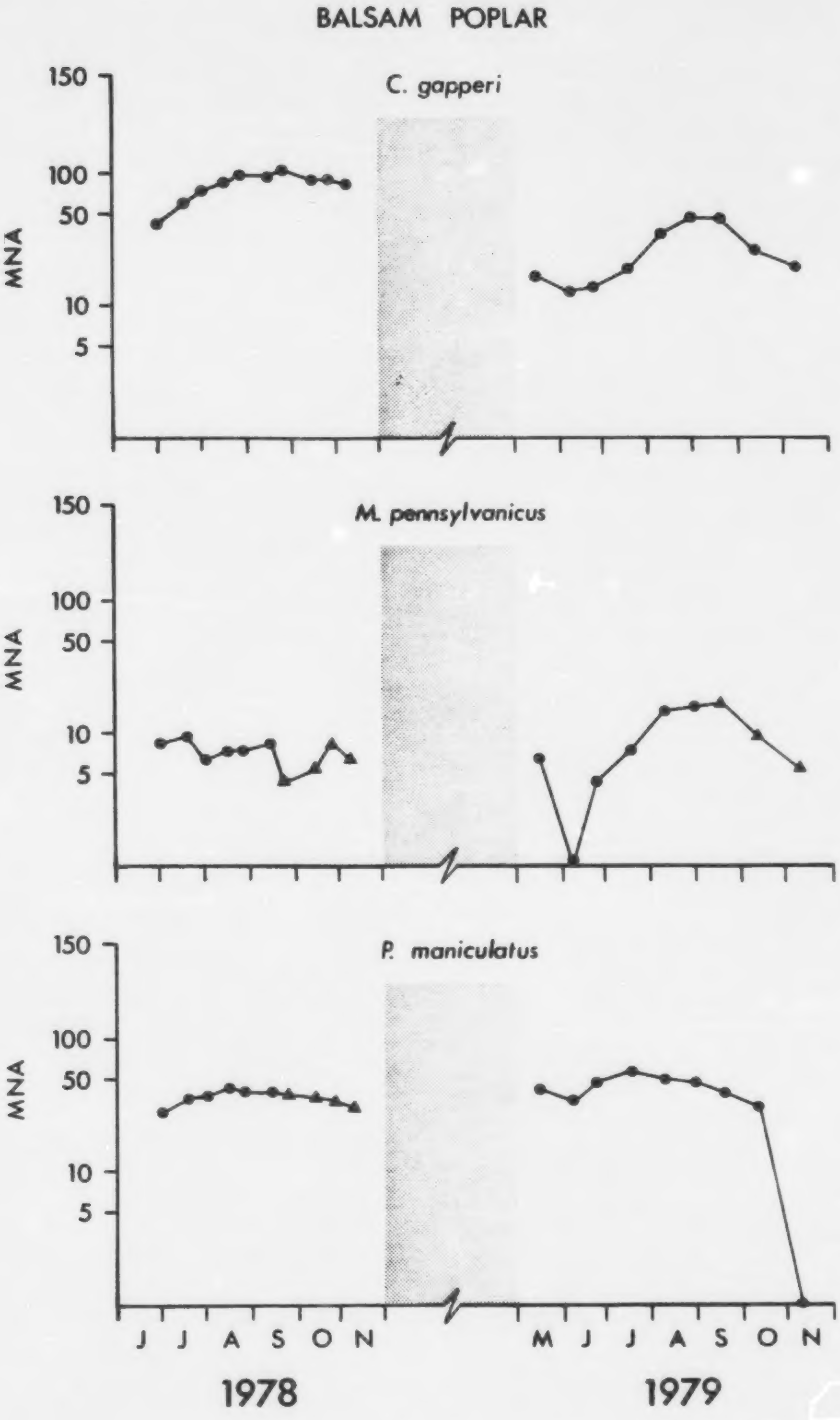

Figure 7. The MNA of small rodents on the Balsam Poplar study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

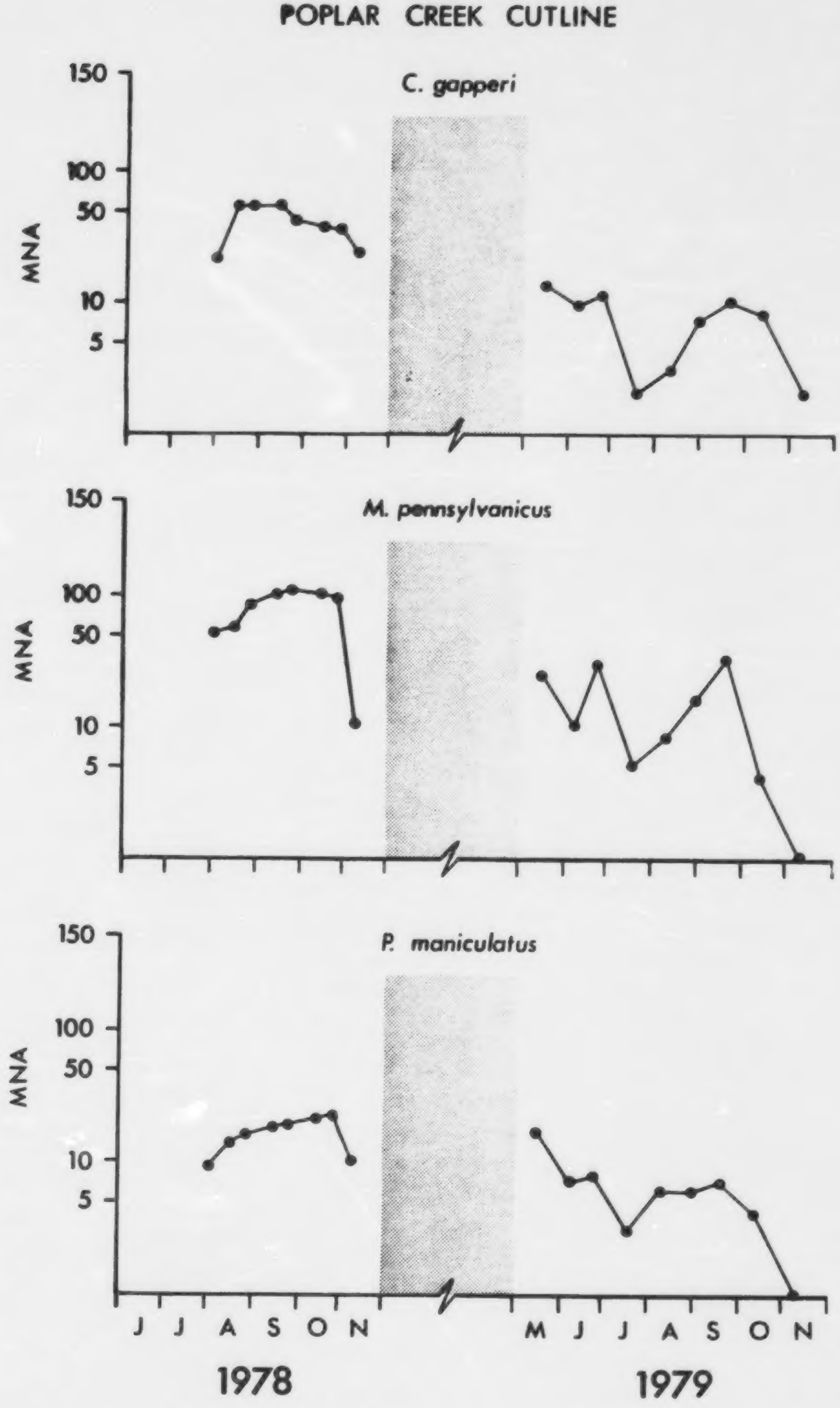

Figure 8. The MNA of small rodents on the Poplar Creek Cutline study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

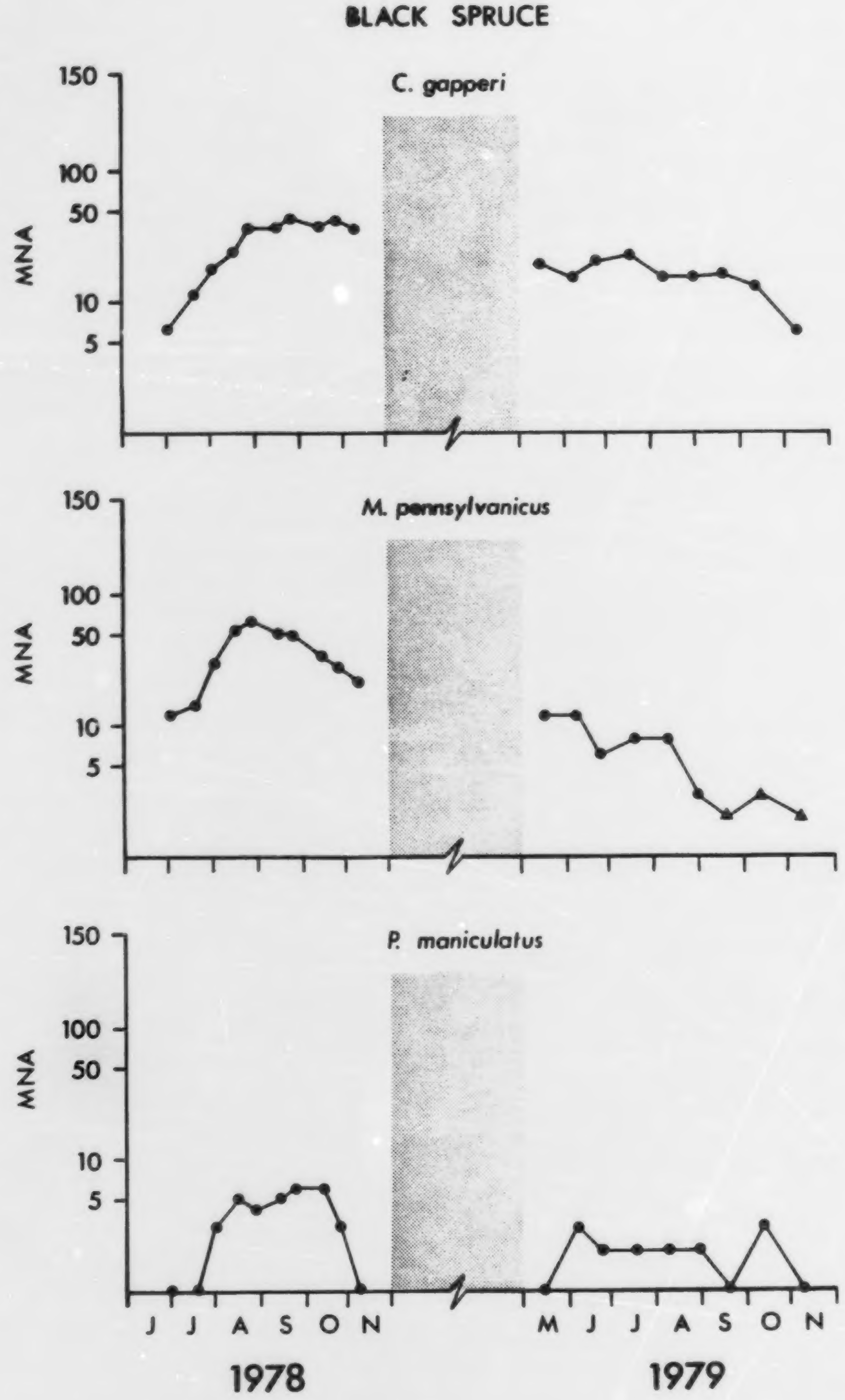

Figure 9. The MNA of small rodents on the Black Spruce study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

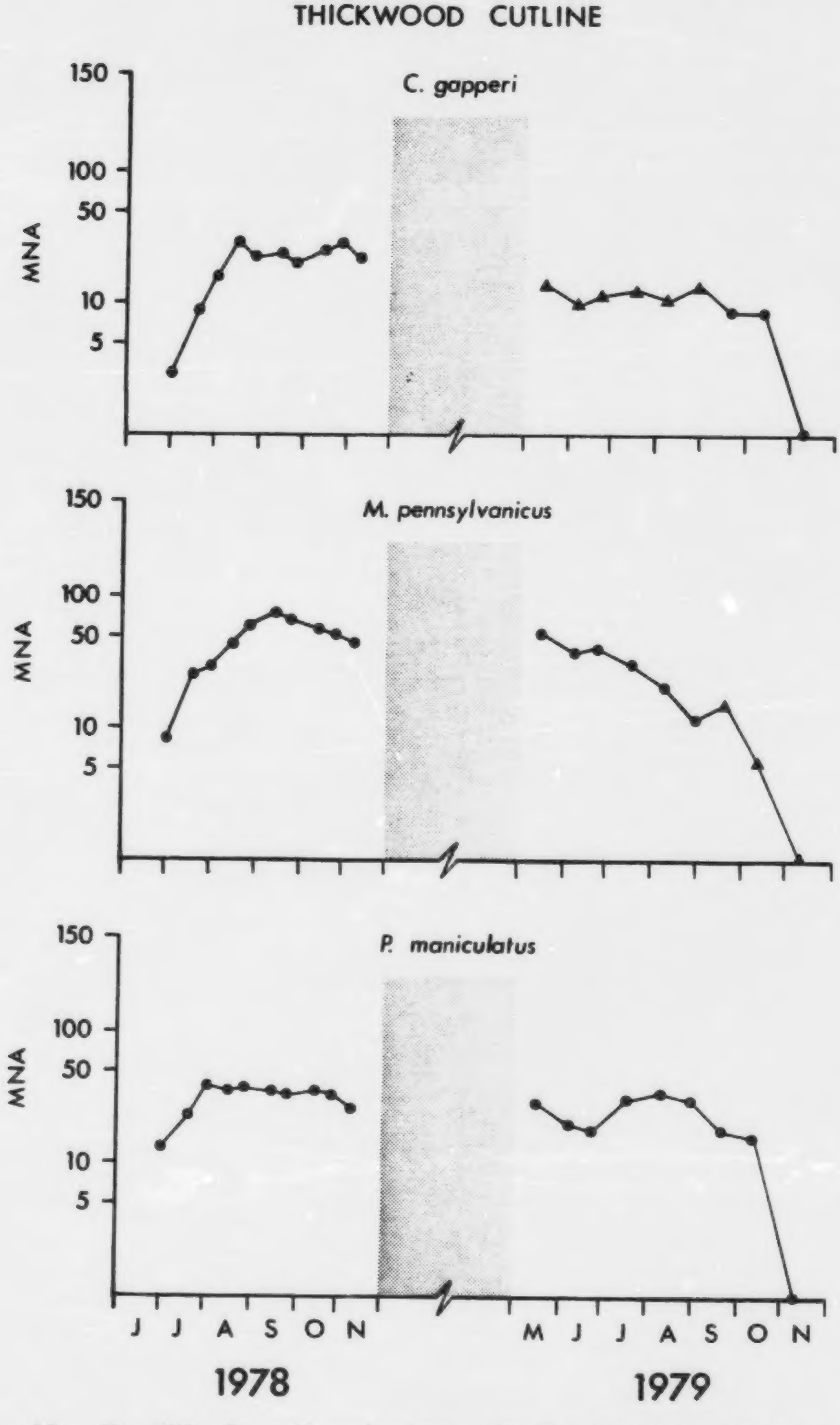

Figure 10. The MNA of small rodents on the Thickwood Cutline study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

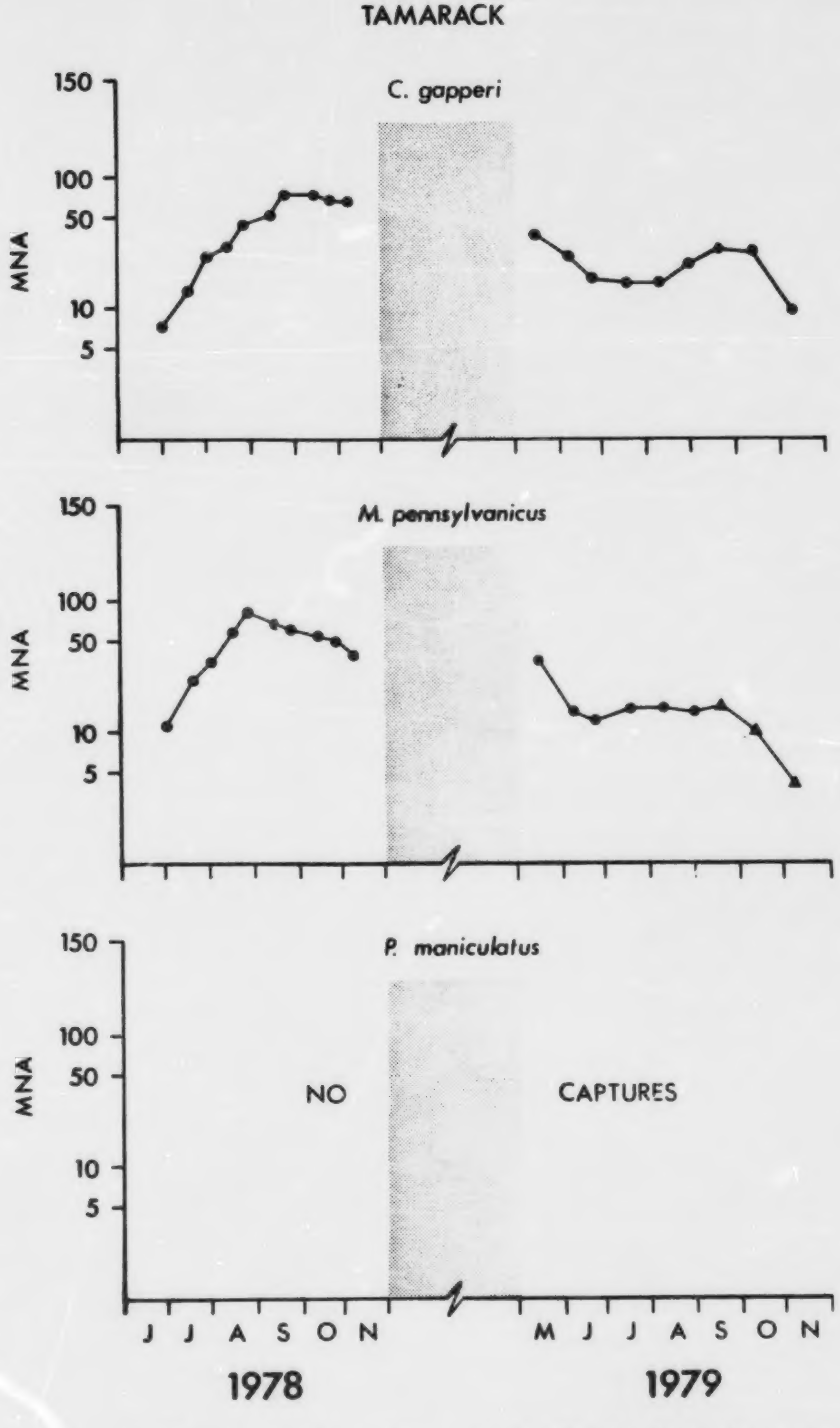

Figure 11. The MNA of small rodents on the Tamarack study area. (Note the log scale. Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size.)

year, but most populations showed no seasonal trends in peak population sizes.

Peromyscus maniculatus was present in moderate densities on the Balsam Poplar and Thickwood Cutline study areas in 1978 and was the most abundant species on the Balsam Poplar and Thickwood Cutline study areas in 1979. No *P. maniculatus* were captured on the Willow or Tamarack study areas in either 1978 or 1979. Peak numbers on the Aspen, Black Spruce, and Thickwood Cutline study areas were similar in 1978 and 1979, whereas populations on the Jack Pine and Poplar Creek cutline areas decreased and the Balsam Poplar population increased. Generally, *P. maniculatus* populations increased most rapidly in July, reached peak numbers in early August, and declined gradually in mid- to late August.

3.2.1.2 Snap-trap censuses. Snap-trap censuses provide crude indices of changes in the abundance of small mammals. However, it is not possible to transform data obtained from linear snap-trap censuses to estimates of density (Calhoun and Casby 1958; Tanaka 1960; Yang et al. 1970).

Snap-trap censuses were used to provide an index of changes in abundance of each of the three major small rodent species in a wider geographic area than that sampled by the live-trapping program. For each species, the mean numbers of animals captured per 100 trap-nights (TN) were used as indices of abundance for each monthly trapping period (Table 3); the number of captures of other small mammal species are summarized in Appendix 11.2, Table 42.

Changes in the mean numbers of animals captured per 100 TN indicate that:

1. *Clethrionomys gapperi* were more abundant in the Athabasca Basin in 1978 than in 1979. In 1978, the number of *C. gapperi* captured was highest in October (snap-trapping was conducted only in July, August, and October). In 1979, the number of *C. gapperi* declined in June, then gradually increased throughout the summer and fall, reaching peak numbers in November.

Table 3. Mean number of animals captured per 100 TN. (The number of TN and the mean number of captures ± 1 S.E. for each month of trapping are indicated.)

Date		TN	*C. gapperi*	*M. pennsylvanicus*	*P. maniculatus*
			Captures/100 TN	Captures/100 TN	Captures/100 TN
1978	July	1748	6.1 ± 1.9	1.8 ± 0.6	1.5 ± 0.7
	August	3231	10.5 ± 1.9	1.3 ± 0.3	1.5 ± 0.5
	October	1205	23.8 ± 3.4	1.5 ± 0.5	3.0 ± 1.6
1979	May	1079	6.5 ± 3.2	0.6 ± 0.4	1.1 ± 0.7
	June	1263	1.4 ± 0.8	0.0	0.4 ± 0.2
	July	1322	1.7 ± 0.4	0.5 ± 0.3	1.1 ± 0.5
	August	1823	5.0 ± 1.3	0.3 ± 0.2	2.8 ± 1.4
	September	1150	7.6 ± 2.6	0.2 ± 0.1	3.2 ± 1.6
	October	1333	6.8 ± 2.1	0.5 ± 0.4	1.7 ± 0.5
	November	1261	9.5 ± 2.0	0.1 ± 0.1	1.0 ± 0.4

2. *Microtus pennsylvanicus* were also more abundant in the Athabasca area in 1978 than in 1979. In 1978, more *M. pennsylvanicus* were captured in July than in the other two sampling periods. In 1979, *M. pennsylvanicus* were most abundant in May and generally declined throughout the summer and fall (the increase in the number of captures of *M. pennsylvanicus* per 100 TN in October was the result of the captures of seven individuals along a cutline in the Thickwood Hills area).
3. The numbers of *P. maniculatus* captured in the Athabasca area did not differ greatly between 1978 and 1979. In 1978, *P. maniculatus* were most abundant in October. In 1979, the number of *P. maniculatus* captured was highest in September.
4. *Clethrionomys gapperi* was the most abundant species of small rodent in the Athabasca Basin in both 1978 and 1979. *Peromyscus maniculatus* and *M. pennsylvanicus* were the second and third most abundant species, respectively, in the Athabasca area.

3.2.1.3 Summary: population changes. The results of both the live-trapping and snap-trapping programs generally indicated the same seasonal and yearly trends in population numbers. *Clethrionomys gapperi* was the most abundant species in most mature forested areas, whereas *M. pennsylvanicus* was most abundant in willow scrub and in the two naturally revegetating areas. *Peromyscus maniculatus* did not occur in either the willow or tamarack areas and was only moderately abundant in the remaining habitats.

Clethrionomys gapperi populations generally declined from higher numbers of animals in 1978 to lower numbers of animals in 1979. Most populations of *C. gapperi* increased rapidly in July and August, reaching peak numbers in late September and October. Snap-trap indices of abundance suggested that peak numbers were reached in October and November. All populations declined over winter.

Microtus pennsylvanicus were abundant in some areas in 1978 but declined in numbers over winter and throughout most of 1979. In 1978, *M. pennsylvanicus* populations increased rapidly in late July and August, reaching peak numbers in late August and September. In 1979, some *M. pennsylvanicus* populations declined steadily throughout the summer and fall. Most populations, however, remained at low numbers throughout the same period.

Peromyscus maniculatus populations showed little change in peak numbers between 1978 and 1979. Most populations began to increase in numbers in July and reached peak numbers in August.

3.3 SURVIVAL AND RECRUITMENT

Changes in the numbers of small rodents within a habitat are a result of population losses (mortality and emigration) and recruitment (births and immigration). Survival and recruitment rates were calculated for each species as a means of assessing the magnitude of population losses and recruitment. Minimum survival rates were calculated as the proportion of animals caught in a trapping period t + 1 (or later on the same grid) that were also caught in trapping period t. Recruitment rates for each grid were calculated, as the proportion of the MNA that were newly tagged on each grid during that trapping period. The trapping season in each year was divided into two seasons, summer (1 July to 20 September 1978 and 16 May to 20 September 1979) and fall (21 September to 9 November 1978 and 21 September to 9 November 1979), and seasonal survival and recruitment estimates were calculated for each species. Because survival and recruitment estimates for each trapping period are ratio estimates and are not independent (i.e., the same animal may occur in two or more samples), it is not appropriate to compare seasons using arithmetic means. Seasonal comparisons therefore were made using multiple regression analyses (MRA) with 'dummy' variables (Johnston 1972) according to the methods described by Fairbairn (1977a).

The following regression model was constructed to estimate seasonal survival rates (a similar analysis was used to estimate seasonal recruitment rates):

$$\begin{aligned}\text{seasonal survival rate} = {} & \text{constant} + B_1(G_2) + B_2(G_3) \ldots\ldots + B_7(G_8) \\ & + B_8(S_2) \\ & + B_9(G_2S_2) + B_{10}(G_3S_2) + \ldots\ldots B_{15}(G_8S_2)\end{aligned}$$

where B_i is the standardized regression coefficient, G_i is the 'dummy' variable for study areas, and S_2 is the 'dummy' variable for the fall period. The terms in the first, second, and third rows of the equation account for effects of study area, season, and season x study area interactions, respectively. Survival estimates were tested for autocorrelation and, where such correlation was found, survival estimates were transformed according to the following equation to correct for this:

$$x_t = x_t - ax_{t-1}$$

where a is the autocorrelation coefficient and x is the survival estimate (Fairbairn 1977). The MRA then was performed on the transformed data. Effects of study area (= habitat type) and season on survival estimates were evaluated by analysis of variance at specific stages of the stepwise multiple regression (Nie et al. 1975). No inter-year comparisons of survival rates were made because of the difference in the frequency of trapping periods (14 days between trapping periods in 1978 and 21 days between trapping periods in 1979).

3.3.1 Seasonal Survival Rates

Survival rates of *C. gapperi* increased between the summer and fall periods of 1978 ($F = 9.67$; 1,62 df; $0.01 > P > 0.001$) but declined between the summer and fall periods of 1979 ($F = 5.20$; 1,63 df; $0.05 > P > 0.01$) (Figure 12). In contrast, comparisons of seasonal survival rates among habitats indicated that differences associated with habitat were not significant in either year (summer 1978: $F = 1.71$; 7,24 df; $P = 0.15$; fall 1978: $F = 1.31$; 7,24 df; $P = 0.29$; summer 1979: $F = 0.32$; 7,40 df; $P = 0.94$; fall 1979: $F = 2.32$; 7,16 df; $P = 0.08$). However, the tendency for survival rates to differ among habitats

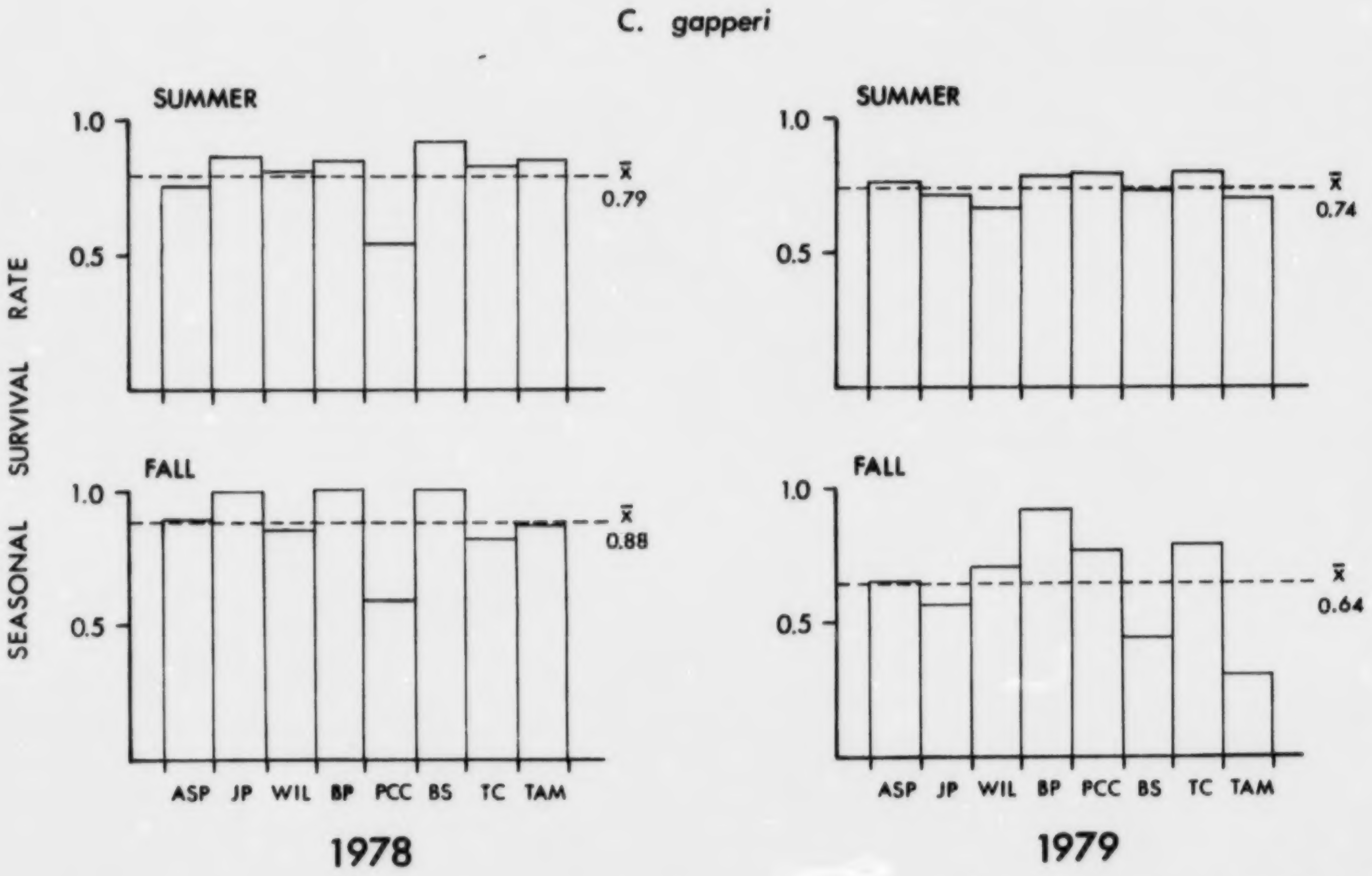

Figure 12. Seasonal survival rates of *C. gapperi*. (Rates shown for each study area are those predicted from MRA described in the text. Abbreviations for study areas are: ASP - Aspen, JP - Jack pine, WIL - Willow, BP - Balsam poplar, PCC - Poplar Creek cutline, BS - Black spruce, TC - Thickwood cutline, TAM - Tamarack.)

during the fall 1979 suggests that animals on the Black Spruce and Tamarack study areas did not survive as well as animals in other habitats. In contrast, survival rates of animals on the Balsam Poplar study area were consistently above average during the summer and fall periods of both years.

Seasonal survival rates of *M. pennsylvanicus* did not change significantly with season in either 1978 or 1979 (1978: $F = 3.90$; 1,62 df; $0.10 > P > 0.05$; 1979: $F = 3.31$; 1,63 df; $0.10 > P > 0.05$) (Figure 13). Seasonal survival rates also did not differ among habitats except during the summer of 1979 (summer 1978: $F = 0.91$; 7,24 df; $P = 0.52$; fall 1978: $F = 0.31$; 7,24 df; $P = 0.94$; summer 1979: $F = 3.58$; 7,40 df; $P = 0.004$; fall 1979: $F = 1.23$; 7,16 df; $P = 0.34$). During the summer of 1979, *M. pennsylvanicus* on the Jack Pine study area survived less well than animals in any other habitat--no *M. pennsylvanicus* survived throughout the summer period of 1979 (Figure 13). Similarly, no *M. pennsylvanicus* on the Jack Pine area survived throughout the fall 1979 period. Survival rates of *M. pennsylvanicus* in willow shrub habitats, however, were consistently above average in all seasons.

Seasonal survival rates of *P. maniculatus* did not differ significantly between the summer and fall periods of 1978 ($F = 0.009$; 1,46 df; $0.75 \geq P > 0.50$) but declined between the summer and fall periods of 1979 ($F = 14.62$; 1,47 df; $0.001 > P$) (Figure 14). Within each season, survival rates of *P. maniculatus* generally did not vary with habitat (summer 1978: $F = 0.20$; 5,18 df; $P = 0.96$; fall 1978: $F = 1.47$; 5,18 df; $F = 0.25$; summer 1979: $F = 2.15$; 5,30 df; $P = 0.09$; fall 1979: $F = 1.03$; 5,12 df; $P = 0.44$), although the tendency for survival rates to differ among the major plant communities during the summer 1979 suggests that *P. maniculatus* survived less well in jack pine forests than in any other habitat. In contrast, seasonal survival rates of animals in balsam poplar and young successional (i.e., Thickwood Cutline study area) habitats were consistently above average during both the summer and fall periods of 1978 and 1979.

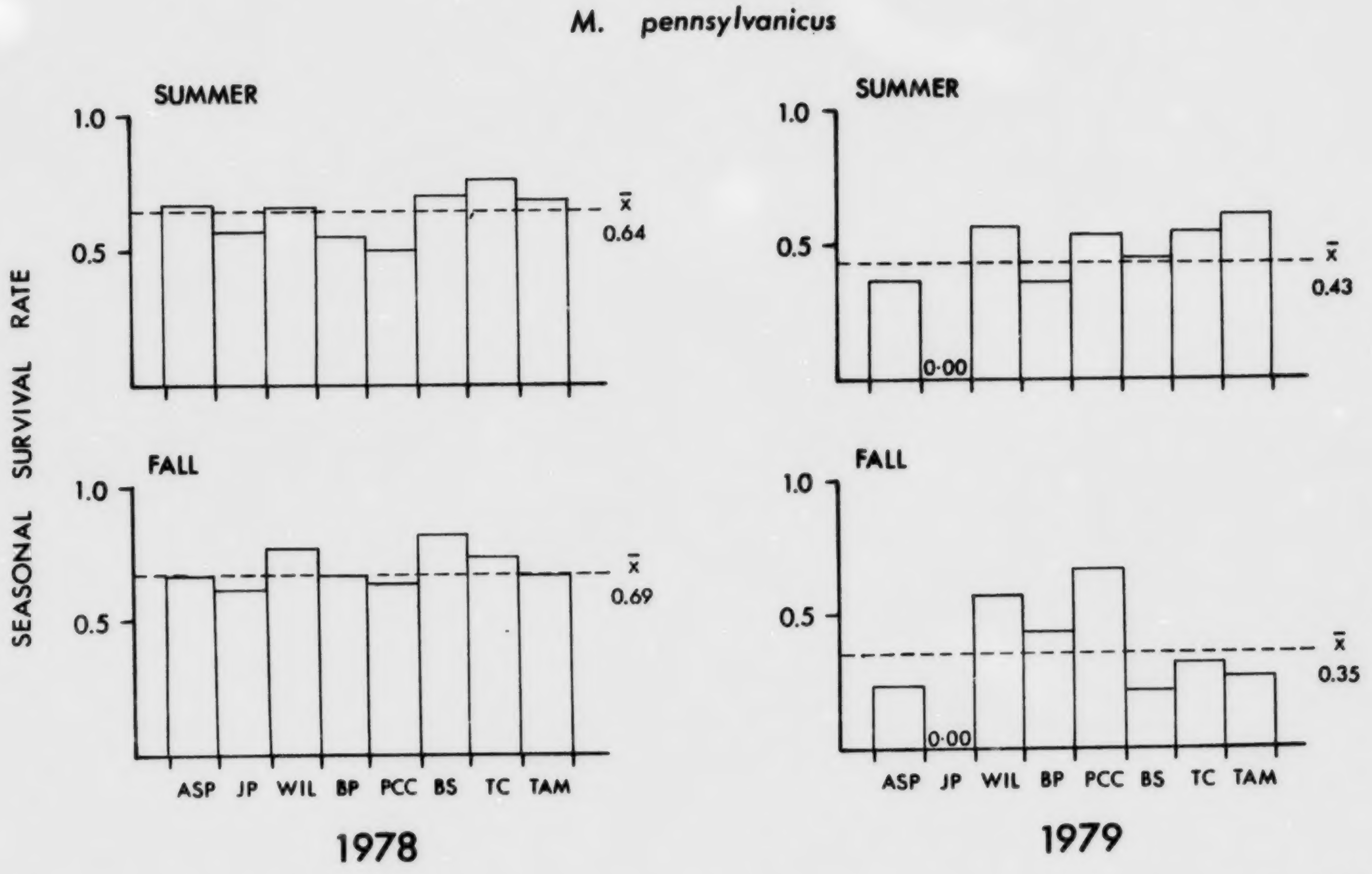

Figure 13. Seasonal survival rates of *M. pennsylvanicus*. (Rates shown for each study area are those predicted from MRA described in the text. See Figure 12 for explanation of study area abbreviations.)

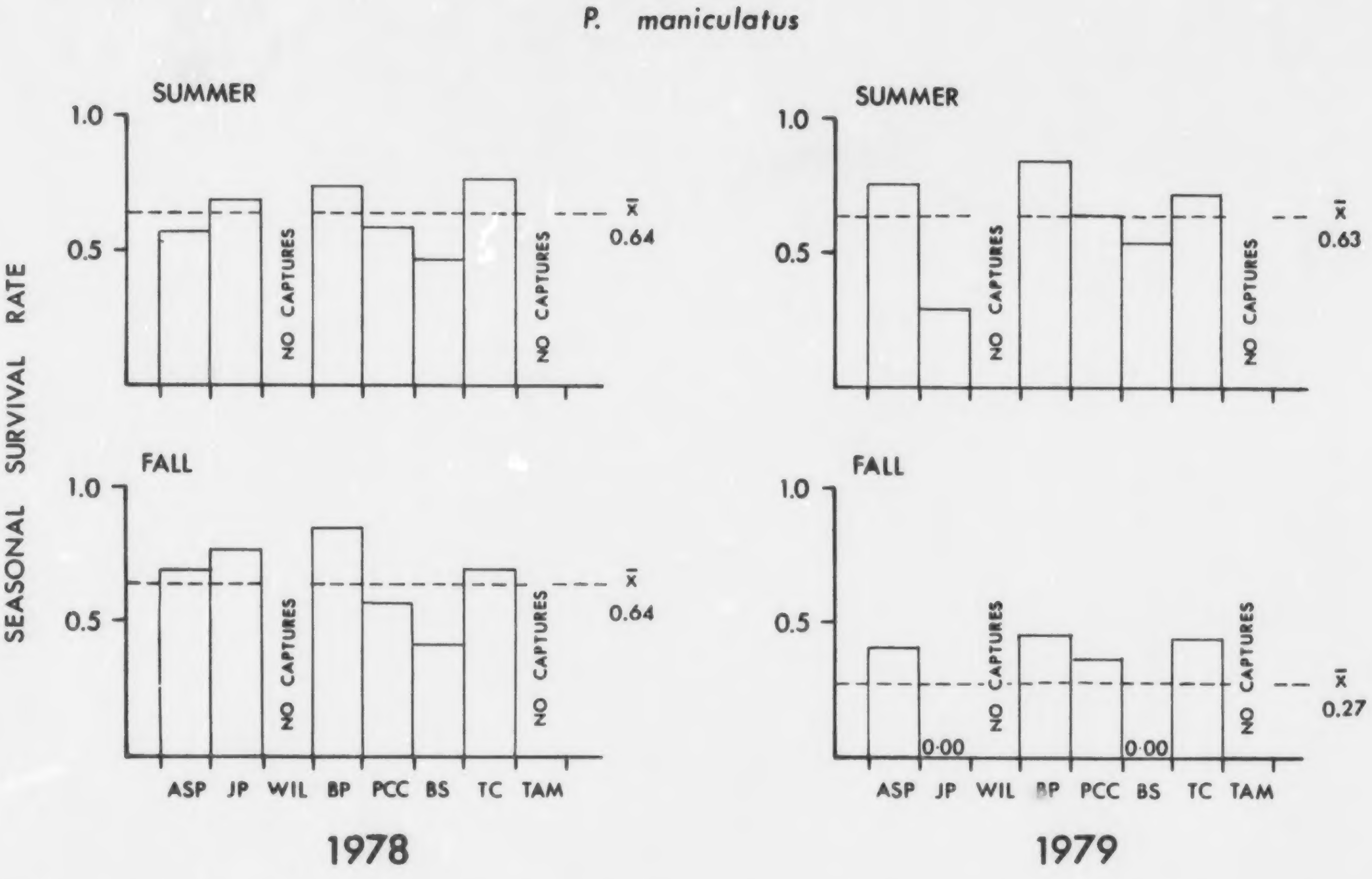

Figure 14. Seasonal survival rates of *P. maniculatus*. (Rates shown for each area are those predicted from MRA described in the text. See Figure 12 for explanation of study area abbreviations. No *P. maniculatus* were captured on the Willow or Tamarack study areas.)

3.3.2 Seasonal Recruitment Rates

Seasonal recruitment rates of *C. gapperi* declined significantly between the summer and fall periods of 1978 (F = 42.08; 1,62 df; 0.001 > P) but did not differ significantly between the summer and fall periods of 1979 (F = 2.40; 1,63 df; 0.25 > P > 0.10) (Figure 15). Within each season, recruitment rates varied widely among the eight study areas but overall recruitment rates did not vary significantly with habitat (summer 1978: F = 0.81; 7,24 df; P = 0.59; fall 1978: F = 1.02; 7,24 df; P = 0.44; summer 1979: F = 0.68; 7,40 df; P = 0.69; fall 1979: F = 0.42; 7,16 df; P = 0.88).

In 1978 and 1979, recruitment rates of *M. pennsylvanicus* decreased between the summer and fall periods--however, this reduction was significant only in 1978 (1978: F = 5.43; 1,62 df; 0.05 > P > 0.01; 1979: F = 1.05; 1,63 df; 0.50 > P > 0.25) (Figure 16). None of the differences in recruitment rates associated with habitat types within each season were significant (summer 1978: F = 1.56; 7,24 df; P = 0.19; fall 1978: F = 1.79; 7,24 df; P = 0.14; summer 1979: F = 0.64; 7,40 df; P = 0.72; fall 1979: F = 0.51; 6,17 df; P = 0.80), although the tendency for recruitment rates of *M. pennsylvanicus* on the Poplar Creek cutline area during the summer and fall 1978 to be above average suggests that recruitment to this population was higher than in any other habitat.

Seasonal recruitment rates of *P. maniculatus* generally were moderate to high during the summer and were quite low during the fall (Figure 17)--reductions in recruitment rates between the summer and fall periods were significant in both years (1978: F = 18.14; 1,46 df; 0.001 > P; 1979: F = 6.71; 1,47 df; 0.05 > P > 0.01). Within each season, recruitment rates generally did not differ significantly among habitats except during the fall 1979 (summer 1978: F = 1.34; 5,18 df; P = 0.29; fall 1978: F = 1.38; 5,18 df; P = 0.28; summer 1979: F = 0.31; 5,30 df; P = 0.90; fall 1979: F = 3.45; 5,12 df; P = 0.04). No animals recruited to the Jack Pine or Black Spruce study areas during the fall 1979, whereas recruitment rates on the Poplar Creek cutline area were greater than in any other area.

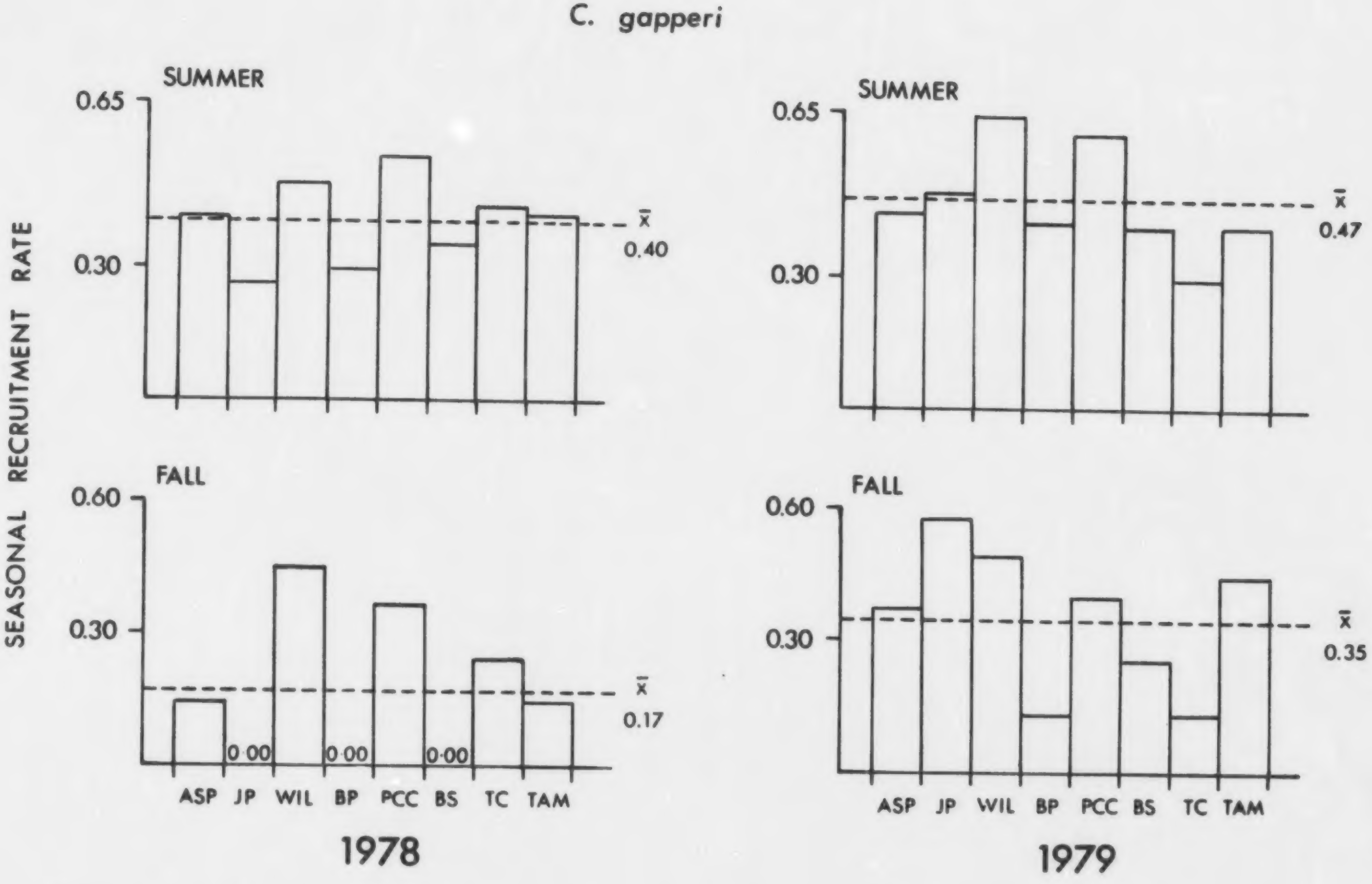

Figure 15. Seasonal recruitment rates of *C. gapperi*. (Rates shown for each area are those predicted from MRA described in text. See Figure 12 for explanation of study area abbreviations.)

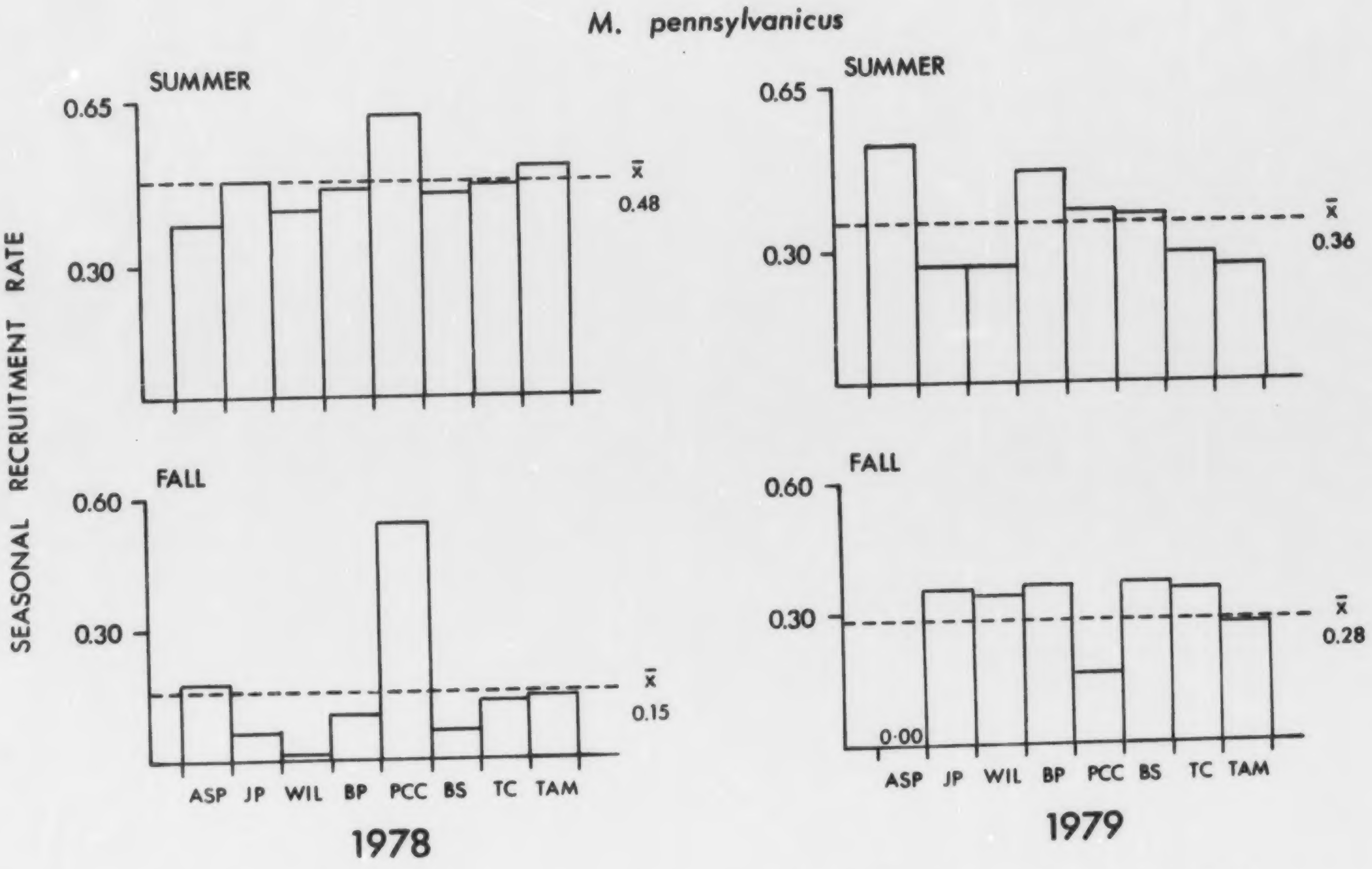

Figure 16. Seasonal recruitment rates of *M. pennsylvanicus*. (Rates shown for each area are those predicted from MRA described in text. See Figure 12 for explanation of study area abbreviations.)

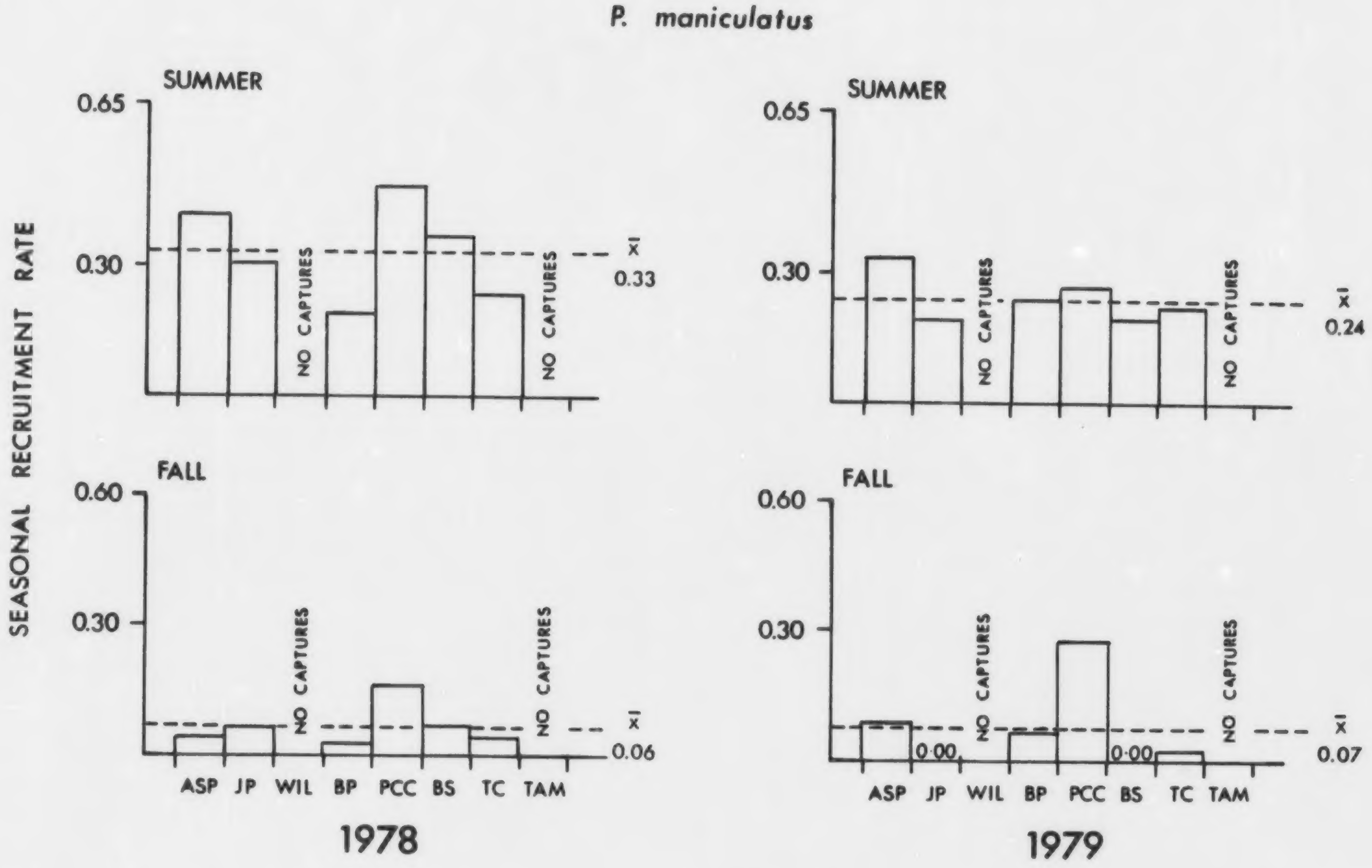

Figure 17. Seasonal recruitment rates of *P. maniculatus*. (Rates shown for each area are those predicted from MRA described in text. See Figure 12 for explanation of study area abbreviations. No *P. maniculatus* were captured on the Willow or Tamarack study areas.)

3.4 POPULATION STRUCTURE

Changes in the age structure or sex ratio of small rodent population can affect reproductive rates and consequently intrinsic rates of increase (Cole 1954; Wilson 1975). For example, increasing populations commonly are characterized by a predominance of younger age classes while stable or declining populations are not (Krebs 1978). Populations with a predominance of females may also have higher reproductive rates than populations with a predominance of males (Williams 1966). Because no reliable techniques are available to accurately age live cricetid rodents from wild populations, age structures were not considered in this study. Sex ratios, expressed as the proportion of animals captured one or more times that were males, were calculated for the three major small rodent species during the summer (1 July to 20 September 1978 and 16 May to 20 September 1979) and fall (21 September to 9 November 1978 and 21 September to 9 November 1979) periods.

Sex ratios of *C. gapperi* in 1978 and 1979 did not differ significantly from 0.5 (chi-square analysis with Yates correction for continuity) on any of the eight study areas during the summer or fall periods (Table 4). However, females were consistently more abundant on the Jack Pine, Balsam Poplar, and Black Spruce study areas throughout 1978 and 1979.

Sex ratios of *M. pennsylvanicus* on each of the eight study areas also did not differ significantly from 0.5 during the summer or fall periods of either year (Table 4). Populations on the Poplar Creek Cutline, Aspen, and Black Spruce study areas, however, generally consisted of more females than males.

Sex ratios of *P. maniculatus* did not differ significantly from 0.5 on any of the six study areas (no *P. maniculatus* were captured on the Willow or Tamarack areas). However, males were consistently more abundant on the Aspen and Balsam study areas, whereas females were consistently more abundant on the Poplar Creek Cutline study area.

Sex ratios, expressed as the proportion of the total number of animals captured that were male, were also calculated for

Table 4. Seasonal sex ratios of small rodents on live-trapping areas. (Sex ratios are expressed as the proportion of animals captured one or more times that were males.)

Species	Season		Aspen		Jack pine		Willow		Balsam Poplar		Poplar Creek Cutline		Black Spruce		Thickwood Cutline		Tamarack	
			R[a]	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N
C. gapperi	summer	1978	0.56	73	0.57	28	0.75	28	0.57	159	0.46	93	0.64	47	0.64	47	0.59	75
	fall	1978	0.49	84	0.55	42	0.64	47	0.54	127	0.43	46	0.68	56	0.62	34	0.48	90
	summer	1979	0.54	105	0.64	66	0.56	32	0.56	100	0.46	26	0.57	58	0.35	31	0.61	83
	fall	1979	0.39	38	0.67	18	0.44	18	0.54	41	0.56	9	0.64	14	0.25	8	0.69	26
M. pennsylvanicus	summer	1978	0.56	16	0.55	38	0.55	104	0.57	21	0.55	151	0.64	87	0.54	100	0.50	122
	fall	1978	0.55	11	0.54	13	0.48	73	0.43	7	0.56	166	0.60	55	0.49	70	0.42	66
	summer	1979	0.50	14	1.00	2	0.51	53	0.49	39	0.56	89	0.50	22	0.45	103	0.51	59
	fall	1979	0.00	1	-	0	0.71	14	0.38	13	0.73	30	0.00	1	0.62	13	0.50	12
P. maniculatus	summer	1978	0.40	30	0.30	10	-	0	0.45	55	0.80	20	0.80	5	0.59	46	-	0
	fall	1973	0.48	21	0.40	5	-	0	0.40	30	0.64	25	0.60	5	0.56	34	-	0
	summer	1979	0.42	26	1.00	2	-	0	0.45	100	0.54	26	0.50	2	0.46	69	-	0
	fall	1979	0.36	11	-	0	-	0	0.42	31	0.67	6	-	0	0.42	12	-	0

[a] Sex ratio.

C. gapperi, *M. pennsylvanicus*, and *P. maniculatus* captured in each major forest cover type during snap trap censuses in July to October 1978 and May to November 1979 (Table 5). Sex ratios of these species did not differ significantly from 0.5 in any major forest cover type.

3.5 REPRODUCTION

Assuming that habitat selection is related to reproductive success, one of the better measures of habitat quality would be the mean number of young within each litter that survives to breeding age. Because of the difficulty in obtaining such a measure in free-ranging populations of small rodents, three indices of reproductive success and reproductive activity were used in this study: the proportions of animals in breeding condition, pregnancy rates, and juvenile recruitment.

3.5.1 Breeding Activity

Male animals captured on live-trapping plots were considered to be in breeding condition if their testes were fully or partially descended (scrotal). Females were considered to be in breeding condition if the vagina was perforate, if nipples were obviously swollen, or if the pubic symphysis was open. Indices of breeding activity, expressed as the proportion of mature males and of mature females that were in breeding condition during the summer period of 1978 (1 July to 20 September) and 1979 (16 May to 20 September), were determined for each species on each grid. Mature animals were defined as animals whose body weights were greater than or equal to 10 g, 16 g, and 14 g for *C. gapperi*, *M. pennsylvanicus*, and *P. maniculatus*, respectively; these weights are based on an analysis of median weights at sexual maturity of animals captured during snap-trap censuses in 1978 (Green 1979b). Proportions of mature male and female animals captured in each trapping period are summarized in Appendix 11.2, Tables 43 to 45.

In 1978, breeding activity of both male and female *C. gapperi* differed significantly among habitats (Friedman's two-way ANOVA;

Table 5. Sex ratios of small rodents captured during snap-trap censuses in the Athabasca Basin. (Sex ratios, expressed as the proportion of the animals captured that were male, are shown for each of the major tree cover types.)

Species	Cover Type[a]	1978 Sex Ratio	1978 N	1979 Sex Ratio	1979 N
C. gapperi	Aspen-white spruce	0.54	282	0.55	193
	Balsam poplar	0.50	28	0.57	61
	Black spruce	0.48	143	0.48	82
	Tamarack	0.67	24	0.71	21
	Balsam fir	0.49	82	0.71	7
	Jack pine	0.00	4	1.00	1
	Paper birch	0.47	73	0.52	31
	Open[b]	0.57	77	0.57	44
M. pennsylvanicus	Aspen-white spruce	0.42	43	0.63	8
	Balsam poplar	-	0	0.67	3
	Black spruce	0.58	12	-	0
	Tamarack	0.00	1	-	0
	Balsam fir	0.57	7	-	0
	Jack pine	-	0	-	0
	Paper birch	0.83	6	1.00	1
	Open[b]	0.51	45	0.46	13
P. maniculatus	Aspen-white spruce	0.52	56	0.64	61
	Balsam poplar	0.50	12	0.50	32
	Black spruce	0.00	1	0.55	11
	Tamarack	-	0	-	0
	Balsam fir	0.67	15	0.50	2
	Jack pine	1.00	2	-	0
	Paper birch	0.67	18	0.57	21
	Open[b]	0.41	17	0.71	28

[a] Each animal was assigned to a cover type based on the dominant tree cover within 10 m of the trap location.

[b] Includes all captures where no trees were present within 10 m of the trap location.

males: $\chi^2 = 20.81$; $N_r = 6$; $K = 7$; $P = 0.004$; females: $\chi^2 = 17.38$; $N_r = 6$; $K = 7$; $P = 0.015$). Breeding activity of males and females on the Willow and Poplar Creek Cutline study areas and of males on the Thickwood Cutline area were lower than in the remaining major habitats. In 1979, however, breeding activity did not differ among study areas (males: $\chi^2 = 4.96$; $N_r = 7$; $K = 7$; $P = 0.66$; females: $\chi^2 = 5.85$; $N_r = 7$; $K = 7$; $P = 0.56$).

Breeding activity of male and female *M. pennsylvanicus* did not differ significantly among habitats in 1978 (males: $\chi^2 = 7.63$; $N_r = 6$; $K = 7$; $P = 0.37$; females: $\chi^2 = 11.89$; $N_r = 6$; $K = 7$; $P = 0.10$) or in 1979 (males: $\chi^2 = 8.22$; $N_r = 7$; $K = 7$; $P = 0.31$; females: $\chi^2 = 4.27$; $N_r = 7$; $K = 7$; $P = 0.64$). In 1978, however, breeding activity of mature female *M. pennsylvanicus* on the Balsam Poplar and Thickwood Cutline study areas tended to be higher than in other habitats.

Breeding activity of *P. maniculatus* also did not differ significantly among habitats in either 1978 (males: $\chi^2 = 1.95$; $N_r = 6$; $K = 5$; $P = 0.86$; females: $\chi^2 = 3.43$; $N_r = 6$; $K = 5$; $P = 0.63$) or 1979 (males: $\chi^2 = 8.74$; $N_r = 7$; $K = 5$; $P = 0.12$; females: $\chi^2 = 2.66$; $N_r = 7$; $K = 4$; $P = 0.62$).

Breeding activity of animals captured during snap-trap censuses was also compared. Indices of breeding activity, as described above, were calculated for animals captured in each of the major forest cover types during the summer of 1979 (July to August 1978) and 1979 (May to August 1979) (Table 6).

Breeding activity of *C. gapperi* was highest in balsam fir, black spruce, and aspen-white spruce forests, whereas breeding activity was limited in areas dominated by paper birch. Few breeding *C. gapperi* were captured in tamarack or jack pine habitats but sample sizes were small.

Numbers of mature *M. pennsylvanicus* were limited in both years. Based on the small numbers captured, breeding activity was highest in habitats with no tree cover or areas dominated by Aspen-white Spruce forest. Few breeding animals were captured in any other habitat.

Because of the late initiation of trapping, few breeding *P. maniculatus* were captured in 1978. In 1979, breeding activity was

Table 6. Breeding activity of small rodents captured during snap-trap censuses in the Athabasca Basin. [Proportions of mature animals that were in breeding condition and numbers of mature animals captured during the summer of 1978 (July and August) and 1979 (May to September) are indicated for each of the major tree cover types.]

		1978				1979			
		Males		Females		Males		Females	
	Cover Type[a]	Prop.	N	Prop.	N	Prop.	N	Prop.	N
C. gapperi	Aspen-white spruce	0.18	108	0.36	90	0.37	49	0.51	43
	Balsam poplar	0.00	2	-	0	0.22	27	0.42	19
	Black spruce	0.21	39	0.24	34	0.64	25	0.53	36
	Tamarack	0.50	2	-	0	-	0	-	0
	Balsam fir	0.57	7	0.50	4	1.00	5	1.00	2
	Jack pine	-	0	1.00	1	0.00	1	-	0
	Paper birch	0.00	17	0.31	16	0.31	13	0.23	13
	Open[b]	0.03	29	0.13	16	0.20	15	0.46	13
M. pennsylvanicus	Aspen-white spruce	0.10	10	0.62	13	0.25	4	0.00	2
	Balsam poplar	-	0	-	0	0.00	2	1.00	1
	Black spruce	0.00	3	0.00	2	-	0	-	0
	Tamarack	-	0	-	0	-	0	-	0
	Balsam fir	0.00	1	-	0	-	0	-	0
	Jack pine	-	0	-	0	-	0	-	0
	Paper birch	0.00	1	0.00	1	0.00	1	-	0
	Open[b]	0.15	13	0.33	9	1.00	2	0.67	3
P. maniculatus	Aspen-white spruce	0.04	24	0.33	18	0.23	26	0.36	14
	Balsam poplar	0.00	2	0.00	1	0.20	10	0.22	9
	Black spruce	-	0	0.00	1	0.75	4	0.50	2
	Tamarack	-	0	-	0	-	0	-	0
	Balsam fir	-	0	-	0	1.00	1	0.00	1
	Jack pine	0.50	2	-	0	-	0	-	0
	Paper birch	0.00	2	0.00	1	0.00	10	0.00	6
	Open[b]	0.00	6	0.00	6	0.50	6	0.33	3

[a] Each animal was assigned to a cover type based on the dominant tree cover within 10 m of the trap location.

[b] Includes all captures where no trees were present within 10 m of the trap location.

highest in black spruce, open, aspen-white spruce, and balsam poplar habitats. During both years, however, aspen-white spruce habitats appeared to more consistently support breeding animals than any other habitat.

Indices of breeding activity in live-trapping areas and from snap-trap censuses suggested that reproductive success of *C. gapperi* was highest in forested habitats as opposed to successional or shrub-dominated habitats. Breeding activity of *M. pennsylvanicus* was highest in successional or open habitats and in balsam poplar and aspen forests, whereas breeding activity of *P. maniculatus* appeared to be most consistent in aspen-white spruce forests.

3.5.2 Pregnancy Rates

Pregnancy rates also are an important index of reproductive condition in polyestrous mammals such as microtine or cricetine rodents. Pregnancy rates, expressed as the proportion of mature female animals captured one or more times during the summer period of 1978 and 1979 (Section 3.5.1) that were pregnant, were calculated for each species on each area.

Pregnancy rates of *C. gapperi* in 1978 were highest on the Thickwood Cutline and Jack Pine study areas and were moderately high on the Aspen, Balsam Poplar, and Black Spruce study areas (Table 7). In 1979, pregnancy rates were again high on the Jack Pine study area and were moderately high on the Black Spruce, Thickwood Cutline, and Aspen study areas.

Pregnancy rates of *M. pennsylvanicus* in 1978 were highest in balsam poplar, jack pine, and young successional habitats (i.e., Thickwood cutline) and were moderately high on the Black Spruce, Aspen, and Willow study areas (Table 7). In 1979, pregnancy rates were highest in aspen habitats followed by young successional, balsam poplar, and tamarack communities.

Pregnant *P. maniculatus* were only captured in several habitats (Table 7). Pregnancy rates were highest on the Thickwood Cutline and Aspen study areas in 1978 and on the Poplar Creek Cutline, Balsam Poplar, and Aspen study areas in 1979.

Table 7. Pregnancy rates of small rodents on live-trapping areas. (Rates are expressed as the proportion of mature females captured one or more times during the summer period that were pregnant.)

Species	Study Area	1978		1979	
		Pregnancy Rate	N	Pregnancy Rate	N
C. gapperi	Aspen	0.31	16	0.19	47
	Jack pine	0.40	10	0.32	22
	Willow	0.17	6	0.07	14
	Balsam poplar	0.30	47	0.12	43
	Poplar Creek cutline	0.16	31	0.15	13
	Black spruce	0.30	10	0.27	22
	Thickwood cutline	0.50	8	0.25	20
	Tamarack	0.11	19	0.06	31
M. pennsylvanicus	Aspen	0.50	2	0.60	5
	Jack pine	0.80	5	0.00	0
	Willow	0.44	16	0.19	21
	Balsam poplar	1.00	3	0.44	18
	Poplar Creek cutline	0.24	41	0.14	36
	Black spruce	0.53	19	0.13	8
	Thickwood cutline	0.74	23	0.55	51
	Tamarack	0.18	33	0.43	28
P. maniculatus	Aspen	0.14	7	0.21	14
	Jack pine	0.00	5	0.00	0
	Willow	-	0	-	0
	Balsam poplar	0.12	17	0.35	52
	Poplar Creek cutline	0.00	2	0.40	10
	Black spruce	0.00	1	0.00	1
	Thickwood cutline	0.30	10	0.19	32
	Tamarack	-	0	-	0

Pregnancy rates were also calculated for mature females captured in snap-trap censuses during the summer period of 1978 and 1979 (Table 8). Pregnancy rates of *C. gapperi* and *P. maniculatus* generally were highest in aspen-white spruce forest, whereas pregnancy rates of *M. pennsylvanicus* appeared highest in both aspen-white spruce and open habitats (however, sample sizes in both years were small).

Based on both live-trapping and snap-trapping information, pregnancy rates of *C. gapperi* were highest in jack pine, successional, and aspen-white spruce habitats. Pregnancy rates of *M. pennsylvanicus* were also high in aspen-white spruce forests as well as in successional habitats and in balsam poplar and jack pine forests. Pregnancy rates of *P. maniculatus* generally were highest in successional habitats and in balsam poplar and aspen-white spruce forests.

3.5.3 Juvenile Recruitment

Juvenile recruitment rates, expressed as the number of new immature animals captured per mature breeding female during each trapping period, were used as a third index of reproductive success. Maturity was determined based on body weights described earlier (Section 3.5.1). Juvenile recruitment rates for each species, summarized in Appendix 11.2, Tables 46 to 48, were compared among habitats using Friedman's two-way ANOVA (Siegel 1956).

Juvenile recruitment rates of *C. gapperi* tended to differ among habitats in 1978 ($\chi^2 = 12.83$; $N_r = 4$; $K = 8$; $0.10 > P > 0.05$) but did not differ significantly among study areas in 1979 ($\chi^2 = 9.53$; $N_r = 6$; $K = 8$; $0.30 > P > 0.20$). Juvenile recruitment tended to be greater in balsam poplar and aspen communities than in any other habitat. Recruitment of juvenile *M. pennsylvanicus* differed among study areas in 1978 ($\chi^2 = 11.15$; $N_r = 3$; $K = 8$; $0.02 > P > 0.01$); juvenile recruitment rates were highest in willow shrub and jack pine forest communities. No significant differences in juvenile recruitment were apparent in 1979 ($\chi^2 = 5.58$; $N_r = 6$; $K = 7$; $0.50 > P > 0.30$). Too few juvenile and mature female *P. maniculatus* were captured in 1978 to allow valid comparisons of juvenile recruitment. In 1979, recruitment rates of juvenile *P. maniculatus* did not differ significantly among several of

Table 8. Pregnancy rates of small rodents captured during snap-trap censuses in the Athabasca Basin. (Rates are expressed as the proportion of mature females, captured one or more times during the summer period, that were pregnant.)

		1978		1979	
Species	Cover Type[a]	Pregnancy Rate	N	Pregnancy Rate	N
C. gapperi	Aspen-white spruce	0.23	32	0.16	43
	Balsam poplar	-	0	0.11	19
	Black spruce	0.18	8	0.06	36
	Tamarack	-	0	-	0
	Balsam fir	0.00	2	0.00	2
	Jack pine	1.00	1	-	0
	Paper birch	0.25	5	0.08	13
	Open[b]	0.13	2	0.15	13
M. pennsylvanicus	Aspen-white spruce	0.38	13	0.00	2
	Balsam poplar	-	0	0.00	1
	Black spruce	0.00	2	-	0
	Tamarack	-	0	-	0
	Balsam fir	-	0	-	0
	Jack pine	-	0	-	0
	Paper birch	0.00	1	-	0
	Open[b]	0.22	9	0.00	3
P. maniculatus	Aspen-white spruce	0.00	18	0.21	14
	Balsam poplar	0.00	1	0.00	9
	Black spruce	0.00	1	0.00	2
	Tamarack	-	0	-	0
	Balsam fir	-	0	0.00	1
	Jack pine	-	0	-	0
	Paper birch	0.00	1	0.00	6
	Open[b]	0.00	6	0.00	3

[a] Each animal was assigned to a cover type based on the dominant tree cover within 10 m of the trap location.

[b] Includes all captures where no trees were present within 10 m of the trap location.

the major habitats (sufficient numbers of *P. maniculatus* for valid comparisons were captured only on the Aspen, Balsam Poplar, Poplar Creek cutline, and Thickwood cutline study areas) ($\chi^2 = 2.75$; $N_r = 6$; $K = 4$; $0.50 > P > 0.30$).

3.6 CONDITION

Habitat use may partially reflect the availability and quality of food resources in an area (Dyke 1971). In turn the quality and quantity of food resources may influence the 'condition' of animals from different habitats. Three indices of condition were used to assess differences in condition between habitats: instantaneous relative growth rates of animals on live-trapping areas, Le Cren's (1951) index of condition, and an index of fat deposition of animals captured during snap-trap censuses.

3.6.1 Growth Rates

Growth rates have been used as indices of condition of *Microtus* spp. and *C. gapperi* (Krebs et al. 1969; Krebs et al. 1973; Fuller 1977). For each species on each study area, weight changes over a 4 wk period were used to calculate regressions of instantaneous relative growth rates versus body weights (Brody 1945). Animals that missed a trapping period or for which weights were not obtained within each 4 wk interval were not included in the analysis for that period. Mean instantaneous relative growth rates were expressed as the proportionate change per day for a standard 25 g mouse and are summarized in Appendix 11.2, Table 49. Overall, there were no significant differences in growth rates between study areas [Friedman's two-way analysis of variance; *C. gapperi* (1978: $\chi^2 = 5.0$; $N_r = 5$; $K = 8$; $P > 0.60$; 1979: $\chi^2 = 7.6$; $N_r = 4$; $K = 8$; $P > 0.35$), *M. pennsylvanicus* (1978: $\chi^2 = 5.0$; $N_r = 5$; $K = 7$; $P > 0.50$; 1979: $\chi^2 = 4.0$; $N_r = 4$; $K = 6$; $P > 0.50$), and *P. maniculatus* (1978: $\chi^2 = 2.6$; $N_r = 5$; $K = 5$; $P > 0.75$; 1979: $\chi^2 = 1.7$; $N_r = 4$; $K = 4$; $P > 0.60$)][1].

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[1] For each analysis, study areas with no growth rate values in more than 50% of the cells were deleted from the analysis.

3.6.2 Le Cren's Index of Condition

Le Cren (1951) developed an index of relative condition based on the ratio of observed weight to weight predicted from body length. Condition factors of this type commonly have been employed in fish population studies. Krebs and Myers (1974) also have applied this index of condition to small rodent population studies.

All body weight and body length data obtained for each species in 1978 and 1979 were pooled to calculate the body weight (Y) - body length (X) regression for each species. Weights of pregnant females were corrected by subtracting the weight of the uterus and embryos from the total body weight. Predicted weights of individual animals were then obtained from the regression. Mean conditions of animals captured in each forest cover type (based on the dominant tree or shrub species at the site of capture) were then determined for each of the three major small rodent species in 1978 and 1979.

In 1978, condition indices of *C. gapperi* varied significantly with habitat types (one-way ANOVA; $F = 6.45$; 7,654 df; $P < 0.001$) (Table 9). *Clethrionomys gapperi* captured in areas dominated by balsam fir or tamarack were in significantly better condition than animals captured in aspen or open cover types (Student-Newman-Keuls multiple-comparisons test; $P < 0.05$). Animals trapped in balsam poplar, black spruce, jack pine, and willow shrub communities were in average condition. Condition indices of *C. gapperi* also varied significantly with forest cover types in 1979 ($F = 3.41$; 7,505 df; $P < 0.001$); *C. gapperi* captured in balsam fir habitats were again in better than average condition.

Condition indices of *M. pennsylvanicus* varied slightly with forest cover types in 1978 ($F = 1.66$; 6,133 df; $P = 0.14$) but showed no significant trends with habitat in 1979 ($F = 0.97$; 3,25 df; $P = 0.42$) (Table 9). Mean indices of condition in 1978 suggested that animals captured in balsam fir cover types were in better condition than animals captured in other cover types.

Table 9. Mean indices of condition of animals captured in snap-trap censuses. [Indices of condition are based on Le Cren's (1951) index of condition. Mean indices of condition are indicated for each of the major habitat types in the AOSERP study area, based on all animals captured in that forest cover type. Mean condition indices ± 1 S.E. and sample sizes are shown.]

Species	Forest Cover Type	1978		1979	
		Mean Index of Condition	N	Mean Index of Condition	N
C. gapperi	Aspen + White spruce	0.98 ± 0.01	270	1.01 ± 0.01	198
	Jack pine	1.08 ± 0.15	4	0.90 -	1
	Willow + birch scrub	1.06 ± 0.03	28	0.94 ± 0.01	91
	Balsam poplar	1.05 ± 0.03	28	1.00 ± 0.02	61
	Black spruce	1.02 ± 0.01	142	0.99 ± 0.01	90
	Tamarack	1.09 ± 0.02	24	0.92 ± 0.03	21
	Balsam fir	1.08 ± 0.01	82	1.05 ± 0.03	7
	Open[a]	0.99 ± 0.02	75	1.02 ± 0.02	44
	All habitats	1.01 ± 0.01	662	0.99 ± 0.01	513
M. pennsylvanicus	Aspen + White spruce	0.99 ± 0.03	42	0.96 ± 0.08	8
	Jack pine	0.76 -	1	- -	0
	Willow + birch scrub	0.99 ± 0.03	34	0.99 ± 0.04	5
	Balsam poplar	- -	0	1.11 ± 0.06	3
	Black spruce	0.93 ± 0.03	12	- -	0
	Tamarack	0.84 -	1	- -	0
	Balsam fir	1.11 ± 0.07	7	- -	0
	Open[a]	1.01 ± 0.02	43	0.98 ± 0.02	13
	All habitats	0.99 ± 0.01	140	0.99 ± 0.03	29
P. maniculatus	Aspen + White spruce	0.97 ± 0.02	55	1.02 ± 0.02	60
	Jack pine	1.05 ± 0.05	2	- -	0
	Willow + birch scrub	1.00 ± 0.05	10	1.03 ± 0.05	7
	Balsam poplar	1.00 ± 0.03	12	1.02 ± 0.02	32
	Black spruce	0.76 -	1	1.08 ± 0.12	19
	Tamarack	- -	0	- -	0
	Balsam fir	1.03 ± 0.03	17	0.93 ± 0.20	2
	Open[a]	0.91 ± 0.02	17	0.97 ± 0.02	28
	All habitats	0.97 ± 0.01	112	1.01 ± 0.01	139

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[a] Open forest cover includes all captures where no trees were present within 10 m of the trap location.

In 1978, condition indices of *P. maniculatus* varied significantly with habitat, whereas no significant relationships were apparent in 1979 (1978: F = 2.21; 6,105 df; $P < .05$; 1979: F = 0.93; 5,133 df; P = 0.47) (Table 9). Multiple comparisons of condition indices in 1978, however, indicated that animals from no one specific habitat type were in significantly (P = 0.05) better condition than animals in other habitat types.

3.6.3 Indices of Fat Deposition

Krebs (1964) used a fat index, based on the amount of fat deposited in the abdominal mesentery, to assess changes in the condition of lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*) during a population cycle. An identical index (1 = no fat to 5 = heavy fat deposits) was used in this study to compare conditions of of animals captured in each of the major forest cover types during snap-trap censuses.

Fat indices of *C. gapperi* varied significantly with habitat in 1978 (Kruskal-Wallis one-way ANOVA[1]: $\chi^2 = 52.04$; 7 df; N = 769; $P < 0.001$). Animals captured in balsam poplar, balsam fir, and tamarack forest tended to have larger deposits of fat, whereas animals captured in jack pine forest had smaller deposits of fat than animals in other habitats (Table 10). No significant differences in amounts of fat deposition among habitats were apparent in 1979 ($\chi^2 = 2.05$; 7 df; N = 512; P = 0.96).

Fat indices of *M. pennsylvanicus* captured in each of the major forest types did not vary significantly in 1978 ($\chi^2 = 5.77$; 7 df; N = 140; P = 0.33) or in 1979 ($\chi^2 = 4.56$; 7 df; N = 29; P = 0.21) (Table 10).

Amounts of fat deposition in *P. maniculatus* captured during snap-trap censuses also did not differ among habitats in 1978 ($\chi^2 = 9.26$; 7 df; N = 112; P = 0.16) but were significantly different in 1979 ($\chi^2 = 19.89$; 7 df; N = 141; P = 0.001). *Peromyscus maniculatus* captured in balsam fir forest had larger deposits of fat than animals

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[1] χ^2 values have been corrected for ties according to Siegel (1956).

Table 10. Mean indices of fat deposition of animals captured in snap-trap censuses. (Mean indices of fat deposition are indicated for each of the major habitat types in the AOSERP study area, based on all animals captured in that forest cover type. Mean indices ± 1 S.E. and sample sizes are shown.)

Species	Forest Cover Type	1978 Mean Fat Index	1978 N	1979 Mean Fat Index	1979 N
C. gapperi	Aspen + White spruce	2.08 ± 0.04	280	1.99 ± 0.03	198
	Jack pine	1.50 ± 0.29	4	2.00 -	1
	Willow + birch scrub	2.28 ± 0.05	130	1.98 ± 0.04	90
	Balsam poplar	2.57 ± 0.13	28	2.03 ± 0.08	61
	Black spruce	2.08 ± 0.05	144	1.97 ± 0.06	90
	Tamarack	2.46 ± 0.10	24	2.05 ± 0.05	21
	Balsam fir	2.49 ± 0.07	82	1.86 ± 0.14	7
	Open[a]	2.17 ± 0.06	77	2.05 ± 0.09	44
	All habitats	2.19 ± 0.02	769	1.99 ± 0.02	512
M. pennsylvanicus	Aspen + White spruce	2.35 ± 0.12	43	2.00 ± 0.19	8
	Jack pine	2.00 -	1	- -	0
	Willow + birch scrub	2.26 ± 0.10	34	2.00 ± 0.00	5
	Balsam poplar	- -	0	1.33 ± 0.58	3
	Black spruce	2.18 ± 0.12	11	- -	0
	Tamarack	2.00 -	1	- -	0
	Balsam fir	2.57 ± 0.20	7	- -	0
	Open[a]	2.09 ± 0.10	43	1.85 ± 0.10	13
	All habitats	2.24 ± 0.06	140	1.86 ± 0.88	29
P. maniculatus	Aspen + White spruce	2.07 ± 0.11	55	1.95 ± 0.07	61
	Jack pine	2.50 ± 0.50	2	- -	0
	Willow + birch scrub	2.70 ± 0.26	10	2.00 ± 0.22	7
	Balsam poplar	2.42 ± 0.15	12	1.97 ± 0.07	32
	Black spruce	2.00 -	1	1.90 ± 0.28	11
	Tamarack	- -	0	- -	0
	Balsam fir	2.27 ± 0.12	15	4.00 ± 0.01	2
	Open[a]	2.18 ± 0.13	17	1.79 ± 0.11	28
	All habitats	2.21 ± 0.07	112	1.95 ± 0.05	141

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[a] Open forest cover includes all captures where no trees were present within 10 m of the trap location.

in other forest cover types, whereas animals captured in open habitats tended to have the lowest fat indices of any groups sampled (Table 10).

3.7 DISCUSSION

3.7.1 Population Trends

Population trends for the three major small rodent species in the AOSERP study area during the period of 1978 to 1979 indicate that *C. gapperi* and *M. pennsylvanicus* populations declined between years, whereas numbers of *P. maniculatus* changed little over the course of the study. Two of these three species (*C. gapperi* and *M. pennsylvanicus*) appear to undergo regular fluctuations in population density [see Krebs and Myers (1974) for a review]. Because of the short duration of this study in relation to the longer term population cycles of *C. gapperi* and *M. pennsylvanicus*, it is not possible to assess adequately the cyclic nature of population changes of these two species in the eight study areas. However, a four-year study of small rodent populations on reclamation sites in the vicinity of Fort McMurray (Radvanyi 1978; Michielsen and Radvanyi 1979) suggests that *M. pennsylvanicus* populations in this region are cyclic and that peak population densities were attained in 1978. Indices of abundance on live-trapping and snap-trapping areas of this study are in agreement with these results--most *M. pennsylvanicus* populations reached peak densities in 1978 and underwent rapid declines between 1978 and 1979.

Peromyscus maniculatus populations, however, may undergo only an annual cycle in numbers (Fuller 1969; Petticrew and Sadlier 1974). Densities of mice typically increase gradually throughout the late spring and summer period, reaching peak numbers shortly after the cessation of breeding when recruitment of juveniles to the population is high (Verts 1957; Petticrew and Sadlier 1974; Fairbairn 1977a, 1978; Sullivan 1979a). Numbers slowly decline throughout the non-breeding period (Petticrew and Sadlier 1974; Fairbairn 1977a), although stress associated with cold fall periods with little snow cover, long, cold winters, and spring meltoff may increase winter mortality in more temperate areas. Population densities are typically low at the onset of breeding in the spring and may decline further depending on the density of the overwintered breeding population (Sadlier 1965; Fairbairn 1977a, 1977b).

Annual cycles such as these were observed in *P. maniculatus* populations on the Aspen, Jack Pine, Black Spruce, and Poplar Creek study areas in 1978 and on the Aspen study area in 1979. Snap-trap indices of *P. maniculatus* abundance in the Athabasca Basin also suggested that numbers of this species increased throughout the summer and reached peak densities in the early fall of each year. Numbers of *P. maniculatus* on the Balsam Poplar and Thickwood Cutline study areas, however, remained almost constant throughout the duration of this study. The poor definition of these annual cycles on almost all study areas in 1979 and the constancy of populations on the Balsam Poplar and Thickwood Cutline study areas indicate that annual cycles in numbers are not a phenomenon common to all populations in all years. Such differences between the study areas further suggest that annual cycles in population size may be influenced by habitat.

3.7.2 Population Characteristics and Habitat Quality

Higher quality habitats should be associated with larger population sizes (Hodgson 1972; Pollard and Relton 1973; Richens 1974; Douglass 1976a; Krebs and Wingate 1976) and high reproductive success (Krebs 1978). Demographic parameters, measured in this study, that are associated most strongly with reproductive success include:

1. High survival rates;
2. High recruitment (recruitment of young born on the area plus immigration);
3. An equal number of males and females in the population or a tendency towards a surplus of females in the population;
4. Moderate to high numbers of mature (breeding) animals during periods of increase;

5. A longer breeding season;
6. High pregnancy rates;
7. High juvenile recruitment to the trappable population; and
8. Better nutritional condition.

However, because some demographic variables are known to vary with cyclic fluctuations in small rodent populations, indices of habitat quality which are based on demographic variables must be used with some caution. For example, increased lengths of breeding seasons, an older age at sexual maturity, high adult and low juvenile survival, high growth rates, larger body weights, and high rates of dispersal all have been associated with increasing small rodent populations [see Krebs and Myers (1974) for a review]. Other variables such as litter size, pregnancy rates, and sex ratios appear to be less sensitive to cyclic changes in population densities. Consequently, comparisons between small rodent populations with asynchronous population fluctuations may incorrectly attribute cyclic changes in some demographic parameters to differences among habitats. To minimize such errors, comparisons were made only among synchronously fluctuating populations of small rodents.

3.7.2.1 Characteristics of *C. gapperi* populations and habitat type. The numbers of *C. gapperi* on each live-trapping area, as well as the numbers of *C. gapperi* captured during snap-trap censuses in the Athabasca valley, declined between 1978 and 1979 suggesting that population fluctuations in this species were synchronous throughout the region. Consequently, comparisons of demographic parameters in each community should reflect differences associated with habitat as opposed to differences associated with asynchronous population changes.

Habitat affinities of small rodents in other boreal forest communities suggest that seasonal variations in habitat availability and habitat use by small rodents as well as peak population numbers are important indices of habitat quality (Douglass 1976a). Population trends offer a means of assessing both the size and stability of small rodent populations in different habitats. In this study, *C. gapperi* were present in all habitat types during both years of the study but the number of animals present and the stability of populations in each habitat differed (Table 11). In 1978, all areas supported moderate to large populations and all populations increased throughout the summer period and early fall. In contrast, only populations on the Aspen, Jack Pine, Balsam Poplar, and Tamarack study areas in 1979 increased during the summer and maintained moderate densities. Overall, this suggests that most mature forested areas (with the exception of black spruce forest cover) were more optimal habitats for *C. gapperi*, whereas successional areas, willow-birch scrub, and black spruce forest were marginal.

Seasonal survival rates and recruitment rates offer another means of assessing population stability. Survival rates reflect the loss of animals from a population as a result of mortality and emigration, whereas recruitment rates reflect the assimilation of new animals into the trappable population through recruitment of animals born on the area and immigration. The individual components of survival and recruitment rates, however, are difficult, if not impossible, to measure under field conditions.

Fairbairn (1977a) suggested a means of evaluating the relative importance of each of these components. Assuming that increased emigration reflects increased movements of animals in the surrounding population, as well as in the study population, then high rates of emigration should be associated with high rates of immigration. Increased movements (dispersal) of animals, as a result, should be characterized by decreased survival and increased recruitment. Conversely, limited dispersal of animals should be characterized by increased survival and decreased recruitment. Other combinations such as low survival rates and poor recruitment rates likely reflect increased mortality, whereas high rates of survival and recruitment probably are associated with in situ natality.

Comparisons of seasonal survival and recruitment rates on each area (Table 11) indicate that dispersal rates of *C. gapperi*

Table 11. Characteristics of *C. gapperi* populations on the eight study areas (July to November 1978 and May to November 1979).

Characteristics	Aspen	Jack pine	Willow	Balsam Poplar
Population trends	- moderate decline between 1978 and 1979; increased annually to Sept.; declined to Oct.	- slight decline between 1978 and 1979; gradual increase throughout summer in both years	- moderate decline between 1978 and 1979; moderate increase during summer and fall 1978, slow increase to Oct. in 1979	- large decline between 1978 and 1979; increased annually to Sept., slight decline in Oct. and Nov.
Peak MNA: 1978	67	29	39	95
1979	38	22	18	43
Sex ratio	- equal	- females more abundant	- equal	- females more abundant
Breeding: Mature males	- average	- average	- low	- average
Mature females	- average	- average	- low	- average
Pregnancy rates	- moderately high	- high	- low	- moderately high
Juvenile recruitment	- above average	- average	- average	- above average
Condition[a]	- moderate to low	- moderate to low	- moderate	- good
Seasonal survival:				
Summer	- average	- average	- average	- slightly above average
Fall	- average	- above average in 1978; average in 1979	- average	- slightly above average
Seasonal Recruitment:				
Summer	- average	- below average in 1978; average in 1979	- above average	- below average
Fall	- average	- below average in 1978; average in 1979	- above average	- below average
Dispersal Index				
Summer	- low	- limited dispersal in 1978; low in 1979	- moderate dispersal	- limited dispersal
Fall	- low	- limited dispersal in 1978; low in 1979	- moderate dispersal	- limited dispersal

continued...

Table 11. Concluded.

Characteristics	Black Spruce	Tamarack	Poplar Creek cutline	Thickwood cutline
Population trends	- moderate decline between 1978 and 1979; gradual increase to Oct. 1978; low numbers and gradual decline in 1979	- marked decline between 1978 and 1979; rapid increase to Oct. 1978; small increase in Aug. and Sept. 1979	- large decline between 1978 and 1979; moderate numbers in summer and fall 1978; very low numbers in 1979	- slight decline between 1978 and 1979; moderate numbers throughout most of 1978; very gradual decline in 1979
Peak MNA: 1978	41	70	52	28
1979	21	34	12	13
Sex Ratio	- females more abundant	- equal	- equal	- equal
Breeding: Mature males	- average	- average	- low	- low
Mature females	- average	- average	- low	- average
Pregnancy rates	- moderately high	- low	- low	- moderate
Juvenile recruitment	- average	- average	- average	- average
Conditions[a]	- moderate	- good	- low	- moderate
Seasonal Survival:				
Summer	- above average in 1978; average in 1979	- average	- poorer than average	- average
Fall	- above average in 1978; below average in 1979	- average in 1978; below average in 1979	- poorer than average	- average
Seasonal Recruitment:				
Summer	- below average	- average	- above average	- slightly above average in 1978; below average in 1979
Fall	- below average	- average in 1978; above average in 1979	- above average	- slightly above average in 1978; below average in 1979
Dispersal Index				
Summer	- limited dispersal	- low	- high dispersal	- moderate dispersal
Fall	- limited dispersal	- low in 1978; high dispersal in 1979	- high dispersal	- moderate dispersal in 1978; limited dispersal in 1979

[a] Based on comparisons of snap-trapping and live-trapping indices of condition.

populations in successional or shrub-dominated habitats (i.e., the Poplar Creek Cutline, Thickwood Cutline, and Willow study areas) were moderate to high in both years of the study, whereas dispersal was limited in all forest cover types. *Clethrionomys gapperi* populations in successional or shrub-dominated areas, as a result, appear to be more transient than those in mature forested areas, suggesting that mature forested areas are higher quality habitat types than successional and shrub-dominated areas.

Indices of reproductive success for *C. gapperi* populations on each of the eight study areas similarly indicated that most mature forest communities were moderate to high quality habitats for this species; reproductive success of animals in mature forest habitats appeared to be higher than that of animals in successional or shrub-dominated communities. Pregnancy rates and breeding activity of animals in willow and successional habitats were low, whereas populations in most forested communities were characterized by moderate to high breeding activity, moderate to high pregnancy rates, and average to above-average juvenile recruitment.

Differences in vegetation among the eight study areas also may have influenced the quality and availability of food on each area and, in turn, influenced the nutritional condition of small rodents. Because nutrition can affect reproductive activity, particularly the length of the breeding season (Batzli and Pitelka 1971; Evans 1973; Cengel et al. 1978; Cole and Batzli 1978; Taitt 1978), indices of condition should offer another means of evaluating habitat quality. Based on the three indices of condition used in this study (growth rates, Le Cren's index of condition, and fat deposition), *C. gapperi* in balsam poplar and tamarack habitats were in better condition than animals in the other major forest cover types. In contrast, *C. gapperi* in older successional areas and in aspen or jack pine forests were in poor condition.

When all characteristics of *C. gapperi* populations are considered, several habitats appear to be consistently better than others. Animals captured in areas dominated by balsam poplar, tamarack, or balsam fir forest cover commonly exhibited characteristics associated with populations in near-optimal habitats; population numbers were moderate to high and remained relatively stable, survival rates were average to good, dispersal from these habitats was low, reproductive success (as measured by several reproductive characteristics) was moderate to high, and nutritional conditions were moderate to high. Conversely, habitats dominated by willow-birch shrub or successional cover appeared to be marginal habitats for this species; populations numbers were low and variable, survival was average to poor, dispersal from these habitats was high, reproductive success was limited, and nutritional conditions were generally moderate to poor. Jack pine, aspen, and black spruce forest cover types appeared to be moderately suitable habitats for *C. gapperi*.

3.7.2.2 Characteristics of *M. pennsylvanicus* populations and habitat type. Snap-trap indices of *M. pennsylvanicus* abundance and peak numbers of this vole on seven of the eight live-trapping areas declined between 1978 and 1979 (Table 12). In contrast, the balsam poplar population increased slightly. Because these population changes appeared asynchronous with populations in other areas, the balsam poplar population was not included in further comparisons of population characteristics among habitats.

Differences in the peak population sizes and population trends of *M. pennsylvanicus* populations on the seven study areas suggest that populations differed among habitats (Table 12). *Microtus pennsylvanicus* were present on all study areas throughout both years of study but were most abundant on the Willow, Tamarack, Poplar Creek Cutline, and Thickwood Cutline study areas. Moderate to high population sizes were most consistent in willow or tamarack communities. In contrast, aspen and jack pine forest communities supported very few *M. pennsylvanicus* in either year. Willow shrub, tamarack forest, and successional communities were most suitable for *M. pennsylvanicus*, whereas aspen and jack pine forests were poor quality habitats for this species.

As previously described for *C. gapperi* populations, indices of dispersal based on comparisons of seasonal survival rates and

Table 12. Characteristics of *M. pennsylvanicus* populations on the eight study areas (July to November 1978 and May to November 1979).

Characteristic	Aspen	Jack pine	Willow	Balsam poplar
Population trends	- very low numbers in 1978 and 1979	- moderately large decline between 1978 and 1979; slight increase to Sept. 1978; very low numbers in 1979	- moderately large decline between 1978 and 1979; increase to peak in late Sept. 1979; slight increase in July 1979	- slight increase in 1978 and 1979; very low numbers in both years
Peak MNA: 1978	12	18	57	8
1979	6	1	22	15
Sex ratios	- females more abundant	- equal	- equal	- equal
Breeding:				
Mature males	- average	- average	- average	- average
Mature females	- average	- average	- average	- above average
Pregnancy rates	- high	- moderately high	- moderate	- high
Juvenile recruitment	- low	- high	- high	- low
Condition[a]	- above average	- average	- above average	- average
Seasonal Survival:				
Summer	- average	- below average	- average to above average	- below average
Fall	- average in 1978; below average in 1979	- below average	- above average	- above average
Seasonal Recruitment:				
Summer	- below average in 1978; average in 1979	- average in 1978; below average in 1979	- below average	- average in 1978; above average in 1979
Fall	- above average in 1978; below in 1979	- below average in 1978; above in 1979	- below average in 1978; above in 1979	- below average in 1978; above in 1979
Dispersal Index:				
Summer	- limited dispersal	- limited dispersal (mortality)	- limited dispersal	- moderate to high dispersal
Fall	- moderate dispersal in 1978; limited in 1979 (increased mortality)	- limited dispersal in 1978 (mortality); high in 1979 (emigration)	- limited dispersal	- limited dispersal

continued...

Table 12. Concluded.

Characteristic	Black Spruce	Tamarack	Poplar Creek cutline	Thickwood cutline
Population trends	- sharp decline between 1978 and 1979; increased rapidly to moderate-high numbers in late Aug. 1978; gradual decline to Nov. 1979	- sharp decline between 1978 and 1979; increased to moderately high numbers in late Aug. 1979 then declined to Nov.; gradual decline throughout 1979	- sharp decline between 1978 and 1979; rapid increase to high numbers to late Sept. followed by rapid decline in fall 1978; increase to mid-Sept. 1979; then declined	- moderate decline between 1978 and 1979; increased to high numbers in mid-Sept. then declined to Nov.; gradual decline throughout 1979
Peak MNA: 1978	62	79	102	73
1979	11	33	32	52
Sex ratios	- females more abundant	- equal	- females more abundant	- equal
Breeding:				
Mature males	- average	- average	- average	- average
Mature females	- average	- average	- average	- above average
Pregnancy rates	- moderate	- moderate	- low	- high
Juvenile recruitment	- moderate	- moderate	- moderate to low	- moderate to low
Condition[a]	- average	- average	- above average	- above average
Seasonal Survival:				
Summer	- average	- above average	- below average in 1978; above in 1979	- above average
Fall	- above average in 1978; below in 1979	- average	- average in 1978; above in 1979	- average
Seasonal Recruitment:				
Summer	- average	- average in 1978; below in 1979	- above average in 1978; average in 1979	- average in 1978; below in 1979
Fall	- below average in 1978; above in 1979	- average	- above average in 1978; below in 1979	- average in 1978; above in 1979
Dispersal Index				
Summer	- limited dispersal	- limited dispersal	- high dispersal in 1978; limited dispersal in 1979	- limited dispersal
Fall	- increased mortality in 1978 high dispersal in 1979 (emigration)	- limited dispersal	- moderate dispersal in 1978; limited dispersal in 1979	- limited dispersal in 1978; moderate dispersal in 1979 (emigration)

[a] Based on comparisons of snap-trapping and live-trapping indices of condition.

recruitment are also useful in assessing the stability of small rodent populations. Dispersal from most *M. pennsylvanicus* populations was low during the summer periods of 1978 and 1979 (Table 12). The only exception was the Poplar Creek cutline population in 1978; dispersal from this population was notably high during the summer of 1978 when the numbers of animals present on this area were greater than on any other study area during this study. During the fall periods of each year, however, increased emigration probably accounted for population declines on several areas, suggesting that forest cover types that were suitable for this species during the summer may be only moderately or marginally suitable habitats during the fall. Emigration appeared to increase in aspen forest and older successional areas during the fall of 1978 and in jack pine forest, black spruce forest, and young successional areas during the fall of 1979.

Assuming that reproductive success is closely associated with habitat quality, indices of reproductive success in this study indicate that young successional, jack pine, and willow habitats were high quality habitats for *M. pennsylvanicus*--populations in these areas were characterized by average to above-average breeding activity and moderate to high pregnancy rates. However, juvenile recruitment was limited in young successional habitats. On the other hand, reproductive success of animals in older successional areas appeared low; breeding activity was average, pregnancy rates were low, and juvenile recruitment was moderate to low.

Because the nutritional condition of an animal can affect reproductive activity, indices of condition should provide a similar measure of habitat quality as reproductive success. Although none of the indices of condition used in this study were significantly associated with habitat differences, trends in snap-trap indices of condition were only partially in agreement with indices of reproductive success. Animals in willow, aspen-white spruce, and open (e.g., successional areas, shrub-dominated areas) habitats appeared to be in better condition than most populations, whereas animals in jack pine and tamarack forest were in poor condition.

If all population characteristics are considered, willow shrub, tamarack forest, and young successional communities appear to be near-optimal habitats for *M. pennsylvanicus*; population numbers were consistently moderate to high, survival was above average, emigration was limited, and reproductive success was high (moderate on the Tamarack study area). No consistent trends in condition were apparent. Conversely, aspen, jack pine, and older successional communities were marginal habitats for this vole; population numbers were variable, survival was average to below average, emigration and mortality were high, reproductive success was low (except in jack pine forest), and indices of condition were poor.

3.7.2.3 Characteristics of *P. maniculatus* populations and habitat types. Differences between population sizes and trends in different habitats of the boreal forest in northeastern Alberta suggest that balsam poplar, young successional, and aspen communities were the most suitable habitats for *P. maniculatus* (Table 13). Jack pine, black spruce, and older successional areas, however, were only marginally adequate. No animals were captured in willow-birch scrub or tamarack cover types.

Dispersal indices generally supported these conclusions (Table 13). Immigration in aspen, jack pine, balsam poplar, and young successional habitats was limited, suggesting that most of the animals present in these communities were animals that had been born on these areas. In contrast, dispersal indices of populations in black spruce and older successional communities were moderate to high. Assuming that higher numbers of transient animals are typical of populations in more marginal habitats, the aspen, jack pine, balsam poplar, and young successional areas are apparently better quality habitats than black spruce and older successional areas.

Reproductive attributes of *P. maniculatus* populations also suggested that balsam poplar, aspen, and successional communities were best-suited for this small rodent, whereas jack pine and black spruce forests were marginal habitats (Table 13). Populations in successional,

Table 13. Characteristics of *P. maniculatus* populations on the eight study areas (July to November 1978 and May to November 1979). (No *P. maniculatus* were captured on either the Willow or Tamarack study areas.)

Characteristics	Aspen	Jack pine	Balsam Poplar
Population trends	- little change between years; seasonal peak in Aug. and Sept.	- low numbers in 1978; very low numbers in 1979	- moderate increase between 1978 and 1979; consistant moderate numbers in 1978; increase to peak in late July and decrease to Nov. 1979
Peak MNA: 1978	22	9	40
1979	15	1	54
Sex ratio	- males more abundant	- equal	- males more abundant
Breeding:			
Mature males	- average	- average	- average
Mature females	- average	- average	- average
Pregnancy rates	- high	- low	- moderately high
Juvenile recruitment	- average	- average	- moderate
Condition[a]	- average	- average	- above average
Seasonal Survival:			
Summer	- slightly below average in 1978; above in 1979	- above average in 1978; below in 1979	- above average
Fall	- above average	- above average in 1978; below in 1979	- above average
Seasonal Recruitment:			
Summer	- above average	- slightly below average	- below average in 1978; average in 1979
Fall	- average	- average in 1978; below in 1979	- below average in 1978; average in 1979
Dispersal Index			
Summer	- moderate to low dispersal in 1978; limited in 1979	- limited dispersal	- limited dispersal
Fall	- limited dispersal	- limited dispersal	- limited dispersal

continued...

Table 13. Concluded.

Characteristics	Black Spruce	Poplar Creek cutline	Thickwood cutline
Population trends	- very low numbers in both years	- moderate decline between 1978 and 1979; increase to low peak in Oct. 1978; low numbers in 1979	- little change between 1978 and 1979; consistent moderate numbers throughout 1978; variable increase to Aug. and decrease to Nov. 1979
Peak MNA: 1978	5	21	38
1979	2	16	34
Sex ratio	- equal	- females more abundant	- equal
Breeding:			
Mature males	- average	- average	- average
Mature females	- average	- average	- average
Pregnancy rates	- low	- moderately high	- moderately high
Juvenile recruitment	- average	- average	- average
Condition[a]	- average	- average	- average
Seasonal Survival:			
Summer	- below average	- average	- above average
Fall	- below average	- average	- above average
Seasonal Recruitment:			
Summer	- average	- above average	- below average in 1978; average in 1979
Fall	- average in 1978; below in 1979	- above average	- below average
Dispersal Index			
Summer	- moderate dispersal	- moderate dispersal	- limited dispersal
Fall	- moderate dispersal in 1978; increased mortality in 1979	- moderate dispersal	- limited dispersal

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[a] Based on snap-trapping and live-trapping indices of condition.

balsam poplar, or aspen communities were characterized by average reproductive activity, average to high pregnancy rates, and moderate juvenile recruitment. In contrast, breeding activity, pregnancy rates, and juvenile recruitment rates were moderate to poor in jack pine and black spruce cover types.

Nutritional conditions of *P. maniculatus*, however, did not appear to be closely associated with habitat types. No differences in growth rates or Le Cren's indices of condition were apparent betweeen populations in the major habitat types. Fat indices, however, did vary significantly among some habitats. Fat deposits of *P. maniculatus* captured in open cover types in 1979 were lower than in other habitats, whereas the fat deposits of animals from areas dominated by balsam fir forest cover were higher than those of animals in other habitats. Successional and shrub-dominated areas, as a result, appear to be poorer quality habitats for this species than other plant communities.

In summary, characteristics of populations in balsam poplar, young successional, and balsam fir communities suggest that these areas were near-optimal habitats for *P. maniculatus*; populations reached moderately high numbers and were relatively stable throughout the summer and fall periods, survival was above average, dispersal was limited, reproductive success was good, and fat indices were high. Older successional areas and jack pine and black spruce forests, however, were marginal habitats; populations generally reached only low to moderate populations sizes, population trends were erratic, survival was generally average to poor, dispersal was moderate to high, reproductive success was moderate to low, and fat deposition was limited. Aspen forest appeared to be a moderately-suitable habitat for *P. maniculatus*. No *P. maniculatus* were captured on the willow or tamarack live-trapping areas in either 1978 or 1979 implying that these communities are unsuitable for this cricetid.

3.8 CONCLUSIONS

Population trends of the three major species of small rodents in the Athabasca Basin suggest that both *C. gapperi* and *M. pennsylvanicus* populations declined between 1978 and 1979, whereas numbers of *P. maniculatus* changed little during the same period. Based on the results of this study and studies by Radvanyi (1978) and Michielsen and Radvanyi (1979), *M. pennsylvanicus* populations reached peak population numbers in 1978 and underwent rapid declines, typical of cyclic microtine populations, in 1979. *Peromyscus maniculatus* populations in some habitats appeared to undergo annual cycles in abundance (typical of this species) but such fluctuations were not common to all populations. Populations that were characteristic of animals in higher quality habitat did not appear to undergo annual cycles in abundance, suggesting that differences in habitat structure (both biotic and abiotic features) may influence annual changes in abundance.

Based on population characteristics of each small rodent species in major habitat types of the boreal forest region of northeastern Alberta, it appeared that balsam fir and balsam poplar forests were moderately to highly suitable habitats for *C. gapperi*, *M. pennsylvanicus*, and *P. maniculatus*. Young successional communities were also near-optimal habitats for the latter two species, whereas tamarack forests were suitable habitats for all species except *P. maniculatus*. In contrast, jack pine forests and older successional communities were only moderate to marginally suitable habitats for the three major species of small rodent. Willow communitites were also marginal habitats for *C. gapperi* and were avoided by *P. maniculatus* yet were optimal habitats for *M. pennsylvanicus*. Aspen and black spruce forests were only moderately suitable habitats for most species.

4. SMALL RODENTS: HABITAT USE

Habitat selection and use by small rodents is the expression of a complex response of an animal to a large number of independent and interdependent variables. Small rodents may respond to intrinsic and/or extrinsic factors which may also vary with season or changes in density. Intrinsic factors may include physiological and behavioural responses, whereas extrinsic factors may include biotic and abiotic environmental cues such as soil types, microclimate, vegetation structure, or interspecific competition. The major objectives of this study were to quantify the habitat affinities of the three major species of small rodents and to assess the relationship between specific components of habitat structure and the abundance of small rodents. By better understanding the habitat affinities of small rodents, the impacts of land disturbances associated with oil sands developments can be more accurately evaluated and more effective mitigative measures can be developed.

Responses of *Clethrionomys gapperi*, *Microtus pennsylvanicus*, and *Peromyscus maniculatus* to the vegetation structure and major habitats of the boreal forest were assessed by three methods: (1) comparisons of the peak population densities of each species in each habitat type; (2) determinations of habitat preferences and avoidances; and (3) multivariate analyses of small rodent abundance and habitat structure.

4.1 PEAK DENSITIES OF SMALL RODENTS

Preferred or optimal habitats have been defined as those habitats where a species is most abundant (e.g., Hodgson 1972; Pollard and Relton 1973; Richens 1974; Douglass 1976a; Krebs and Wingate 1976). In this study, peak population densities were used as one index of habitat use.

Clethrionomys gapperi were most abundant in areas dominated by balsam poplar (*Populus balsamifera*) (Table 14) and were less abundant in trembling aspen-white spruce forest (*Populus tremuloides* and *Picea glauca*, respectively) and tamarack forest (*Larix laricina*).

Table 14. Peak MNA estimates for each study area. (MNA estimates were calculated as described in Section 3.2.1.1.)

Grid	Peak MNA Estimate					
	C. gapperi		*M. pennsylvanicus*		*P. maniculatus*	
	1978	1979	1978	1979	1978	1979
Aspen	67	38	12	6	22	15
Jack Pine	29	22	18	1	9	1
Willow	39	18	57	22	-	-
Balsam Poplar	95	43	8	15	40	54
Poplar Creek Cutline	52	12	102	32	21	16
Black Spruce	41	21	62	11	5	2
Thickwood Cutline	28	13	73	52	38	34
Tamarack	70	34	79	33	-	-

Moderate numbers of *C. gapperi* were present in black spruce forest (*Picea mariana*), jack pine forest (*Pinus banksiana*), willow scrub (*Salix* spp.), and young successional areas (the two cutline study areas).

Microtus pennsylvanicus were most common in successional areas or sites dominated by tamarack forest or willow scrub. Few animals were present in areas dominated by black spruce forest, balsam poplar forest, aspen-white spruce forest, or jack pine forest.

Peromyscus maniculatus were most abundant in areas dominated by balsam poplar forest, and were moderately abundant in successional areas and in aspen-white spruce forest. Few *P. maniculatus* inhabited areas dominated by jack pine forest or black spruce forest and none were captured in willow or tamarack habitats.

4.2 HABITAT USE AND AVAILABILITY

Habitat preferences of the major species of small rodent in northeastern Alberta were assessed by comparisons of indices of habitat use and availability that were obtained during the two-year snap-trap census program (Section 3.1.2). Habitat availability was estimated by recording the dominant tree and shrub species within a 5 m radius of each of the 20 trap stations along each snap-trap census line; the tree and shrub species with the highest percent coverage (based on the area of the canopy) of the sampling area was recorded as the dominant species. For each mouse captured during a snap-trap census, the dominant tree and shrub species within 5 m of the trap were also recorded. Habitat use by each of the small rodent species was estimated using the number of captures in each of the tree and shrub cover types. The statistical significance of preferences for or avoidances of specific forest cover types or specific shrub understories were determined using the technique described by Neu et al. (1974).

In 1978, *C. gapperi* preferred areas with no tree cover or treed areas dominated by *Abies balsamea* or *Betula* spp. and avoided habitats dominated by *P. tremuloides*, *P. mariana*, or *P. banksiana*

(Table 15). In 1979, *C. gapperi* selected *P. balsamifera*, *P. glauca*, or *L. laricina* forest cover types over other habitats and again avoided communities dominated by *P. mariana*. Understory areas dominated by *Rosa* spp. were preferred by *C. gapperi* in 1978, whereas areas of shrub understory dominated by *Salix* spp. or *Amelanchier alnifolia* were avoided (Table 16). Understory habitats dominated by *Betula glandulosa*, *Alnus* spp., and *Viburnum* spp. were most preferred in 1979. As in 1978, areas dominated by *Salix* spp., as well as areas with no shrub cover, were avoided.

Microtus pennsylvanicus showed a significance preference in both 1978 and 1979 for unforested areas (areas with no tree cover such as young successional areas, shrub thickets, clearings, and marsh edges) and consistently avoided forested areas dominated by *P. mariana* (Table 15). Understory areas with a predominance of *Rubus melanolasius* were preferred by *M. pennsylvanicus* in 1978, whereas understory habitats dominated by *Cornus stolonifera* were avoided (Table 16). Although the distribution of *M. pennsylvanicus* captures in 1979 did differ significantly from that expected by chance, no preferences for or avoidances of specific shrub cover types were apparent ($P = 0.05$).

Peromyscus maniculatus showed few preferences for any forest cover or shrub cover type (Tables 15 and 16); in 1978 and 1979, this species preferred treed areas dominated by *A. balsamea* and *P. balsamifera*, respectively, and avoided *P. mariana* forest cover in both years. Use of most shrub cover types by *P. maniculatus* was proportionate to their availability--however, areas dominated by *Salix* spp. and *B. glandulosa* were inhabited less commonly by *P. maniculatus* in 1978 than expected. In 1979, *P. maniculatus* preferred shrub cover types dominated by *Alnus* spp. and avoided areas dominated by *Salix* spp.

4.3 HABITAT STRUCTURE AND SMALL RODENT ABUNDANCE

Use of boreal forest habitats by small rodents may be influenced by a number of factors related to vegetation structure or microhabitat differences. Variation in these factors may not be

Table 15. Habitat preferences of small rodents related to forest cover types. (Chi-square values for each species in each year were: *C. gapperi*--1978: $\chi^2 = 148.9$; $P < 0.001$; 1979: $\chi^2 = 93.9$; $P < 0.001$; *M. pennsylvanicus*--1978: $\chi^2 = 202.4$; $P < 0.001$; 1979: $\chi^2 = 36.5$; $P < 0.001$; *P. maniculatus*--1978: $\chi^2 = 88.6$; $P < 0.001$; 1979: $\chi^2 = 77.1$; $P < 0.001$.)

		C. gapperi		*M. pennsylvanicus*		*P. maniculatus*	
Species	Proportion of All Habitats Sampled	Proportion of Total Observed Captures[a]	Habitat Use[b]	Proportion of Total Observed Captures[c]	Habitat Use[b]	Proportion of Total Observed Captures[d]	Habitat Use[b]
1978							
P. tremuloides	0.195	0.146	-	0.140	0	0.195	0
P. balsamifera	0.038	0.040	0	0.000	N	0.089	0
P. glauca	0.261	0.245	0	0.264	0	0.260	0
P. mariana	0.278	0.201	-	0.099	-	0.008	-
L. laricina	0.021	0.039	0	0.017	0	0.000	N
A. balsamea	0.049	0.115	+	0.058	0	0.147	+
P. banksiana	0.025	0.005	-	0.008	0	0.016	0
Betula spp.	0.069	0.101	+	0.041	0	0.147	0
No trees	0.064	0.108	+	0.373	+	0.138	0
1979							
P. tremuloides	0.214	0.172	0	0.172	0	0.265	0
P. balsamifera	0.082	0.137	+	0.104	0	0.203	+
P. glauca	0.194	0.256	+	0.172	0	0.133	0
P. mariana	0.285	0.197	-	0.034	-	0.063	-
L. laricina	0.014	0.050	+	0.000	N	0.000	N
A. balsamea	0.008	0.017	0	0.000	N	0.013	0
P. banksiana	0.003	0.002	0	0.000	N	0.000	N
Betula spp.	0.076	0.068	0	0.034	0	0.146	0
No trees	0.124	0.101	0	0.484	+	0.177	0

[a] Based on a total of 751 captures in 1978 and 489 captures in 1979.

[b] Habitat use related to habitat availability:
0 use not significantly different from availability
- use significantly less than availability
+ use significantly greater than availability
N confidence interval cannot be calculated for a zero value.

[c] Based on a total of 121 captures in 1978 and 29 captures in 1979.

[d] Based on a total of 123 captures in 1978 and 158 captures in 1979.

Table 16. Habitat preferences of small rodents related to shrub cover types. (Chi-square values for each species in each year were: *C. gapperi*--1978: $\chi^2 = 175.2$; $P < 0.001$; 1979: $\chi^2 = 74.2$; $P < 0.001$; *M. pennsylvanicus*--1978: $\chi^2 = 99.8$; $P < 0.001$; 1979: $\chi^2 = 48.2$; $P < 0.001$; *P. maniculatus*--1978: $\chi^2 = 75.9$; $P < 0.001$; 1979: $\chi^2 = 129.2$; $P < 0.001$.)

		C. gapperi		*M. pennsylvanicus*		*P. maniculatus*	
Species	Proportion of All Habitats Sampled	Proportion of Total Observed Captures[a]	Habitat Use[b]	Proportion of Total Observed Captures[c]	Habitat Use[b]	Proportion of Total Observed Captures[d]	Habitat Use[b]
1978							
Salix spp.	0.241	0.113	-	0.158	0	0.057	-
B. glandulosa	0.080	0.074	0	0.150	0	0.016	-
Alnus spp.	0.287	0.273	0	0.258	0	0.359	0
A. alnifolia	0.014	0.003	-	0.000	N	0.008	0
Rosa spp.	0.067	0.108	+	0.100	0	0.146	0
C. stolonifera	0.035	0.033	0	0.008	-	0.049	0
Ribes spp.	0.010	0.011	0	0.017	0	0.024	0
S. canadensis	0.020	0.017	0	0.017	0	0.000	N
Viburnum spp.	0.137	0.140	0	0.108	0	0.203	0
R. melanolasius	0.010	0.025	0	0.092	+	0.057	0
No shrubs	0.101	0.203	0	0.092	0	0.081	0
1979							
Salix spp.	0.200	0.108	-	0.207	0	0.045	-
B. glandulosa	0.051	0.093	+	0.000	N	0.000	N
Alnus spp.	0.228	0.301	+	0.207	0	0.410	+
A. alnifolia	0.005	0.006	0	0.000	N	0.051	0
Rosa spp.	0.162	0.153	0	0.103	N	0.141	0
C. stolonifera	0.054	0.037	0	0.000	N	0.090	0
Ribes spp.	0.014	0.008	0	0.034	0	0.000	N
S. canadensis	0.035	0.039	0	0.034	0	0.013	0
S. albus	0.004	0.006	0	0.000	0	0.000	N
Viburnum spp.	0.094	0.143	+	0.103	0	0.135	0
R. melanolasius	0.015	0.017	0	0.172	0	0.019	0
No shrubs	0.138	0.089	-	0.138	0	0.096	0

[a] Based on total of 751 captures in 1978 and 483 captures in 1979.

[b] Habitat use related to habitat availability:

0 use not significantly different from availability
- use significantly less than availability
+ use significantly greater than availability
N confidence interval cannot be calculated for a zero value.

[c] Based on a total of 121 captures in 1978 and 29 captures in 1979.

[d] Based on a total of 123 captures in 1978 and 158 captures in 1979.

defined accurately by the major discrete habitat types identified in the AOSERP study area [as described by Stringer (1976)], largely because the values of these variables are continuously distributed rather than discrete. In addition, other factors that are not used in the categorization of these major habitat types nevertheless may be important in determining the distribution and abundance of a particular species of small rodent. In this study, multivariate statistical techniques were used as one means of assessing the relationship between habitat structure and small rodent habitat use on each of the live-trapping areas. Such statistical techniques permit the simultaneous consideration of all habitat data and so avoid the necessity for arbitrary classifications of habitat types.

4.3.1 Quantification of Habitat Structure and Rodent Abundance

Vegetation analyses on live-trapping areas were conducted during the period of 25 June to 30 July 1978 and 23 to 30 June 1979. Estimates were made of (1) sapling density and species composition of saplings and (2) density, species composition, and vertical composition of ground cover. At each of 30 random sample points on each study area, a 4 m x 4 m quadrat and a 1 m x 1 m quadrat were placed on the ground as shown in Figure 18.

Sapling densities were estimated by counting the number of each species of tree and shrub present in the 16 m^2 quadrat. Saplings were defined as individual young trees with a stem diameter of 3 cm or less at a height of 15 cm above ground level. Each distinct shrub (i.e., a distinct grouping of stems at ground level) was also counted as one plant. In 1979, the total number of stems of each tree and shrub species in the quadrat was also recorded.

Estimates of the percent ground coverage (on the horizontal plane) of each plant species and ground litter within the 1 m^2 quadrats were obtained using a Braun-Blanquet cover scale (Kershaw 1966).

The density (percent cover) of all vegetation in each 0.25 m vertical increment was estimated visually at two opposite corners of the 1 m^2 quadrat (Figure 18) using the vegetation profile board

F2

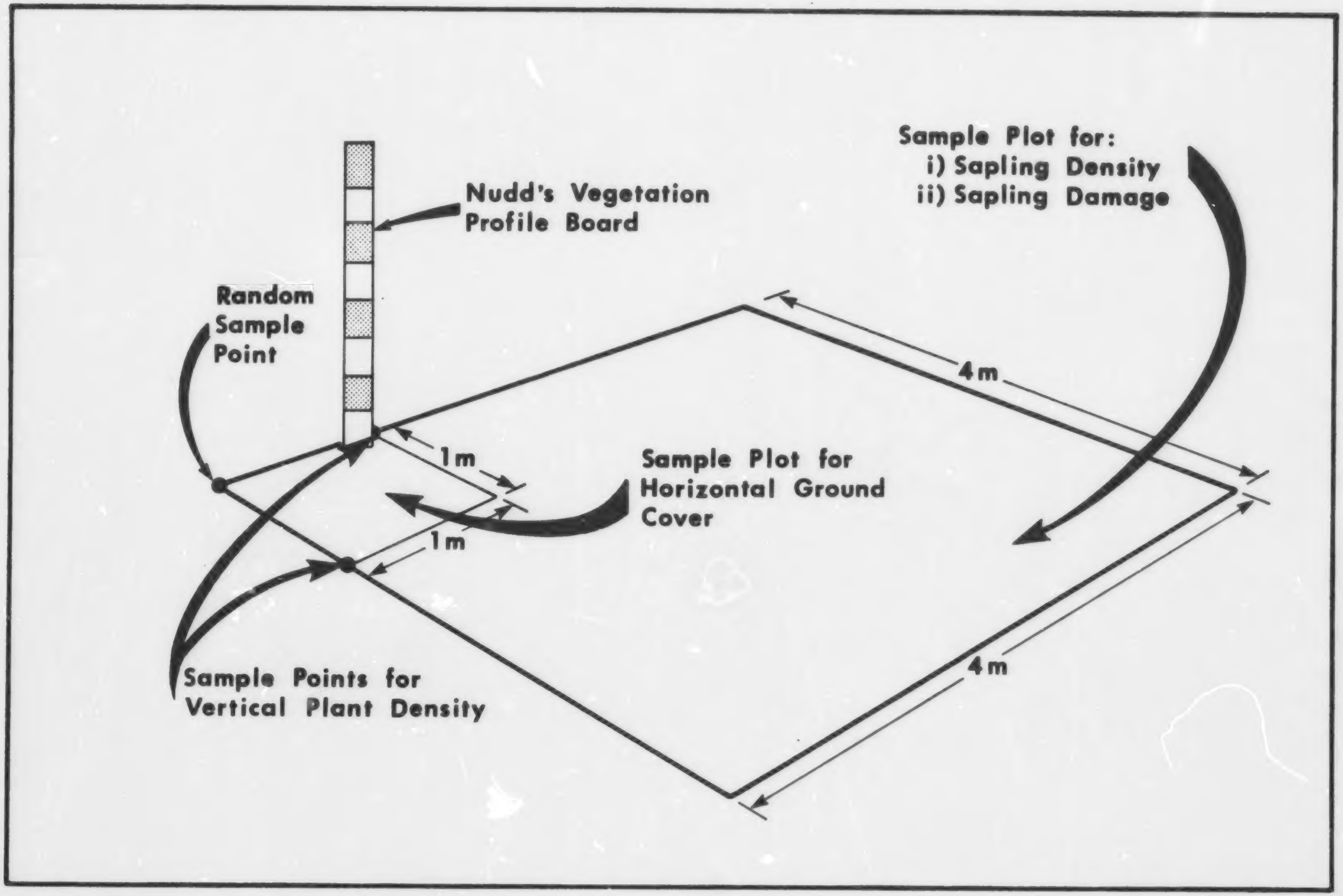

Sample Plot for:
i) Sapling Density
ii) Sapling Damage
Nudd's Vegetation Profile Board
Random Sample Point
4 m
1 m
Sample Plot for Horizontal Ground Cover
1 m
4 m
Sample Points for Vertical Plant Density

Figure 18. The configuration of vegetation sampling quadrats. (The 16 m^2 sampling quadrat, the 1 m^2 quadrat, and the vertical cover sample points are shown.)

method of Nudds (1977). More specific information on vertical plant cover was collected for each of the three most dominant plant species in the 1 m^2 quadrat (based on the estimates of percent horizontal cover). For each dominant species, the vertical zone with the highest density of cover was first estimated and the minimum height of this zone (from the ground surface) was recorded. Two minimum heights for each dominant species were obtained--one at each of the two corners of the quadrat sampled for vertical cover. The depth of the plant litter (i.e., dead grasses, twigs, leaves, etc.) was also measured at each of these two sample points.

The total number of captures per trap night (CTN) for the four closest trap-stations to each vegetation sample was used as an index of small rodent abundance. Because information on vegetation structure was collected in June of each year and consequently was representative of summer vegetation structure, indices of small mammal abundance were calculated only for the period 1 July to 27 August 1978 (except for Grid 5 where only the period 1 August to 27 August was considered) and for the period 24 June to 31 August 1979. Estimates of the cumulative CTN for *C. gapperi* and *M. pennsylvanicus* were based on three trap checks (= nights) per trapping period minus any trap setoffs during that period (e.g., accidental closure of traps, captures of other species of small rodents, birds, and reptiles). Because *P. maniculatus* is nocturnal, numbers of trap nights were based on only two trap checks per trapping period minus any trap setoffs.

4.3.2 Multi-variate Analyses of Habitat Structure and Small Rodent Abundances

Two techniques were used to assess the relationship between small rodent abundance and vegetation. Initially factor analyses were used to reduce 216 habitat variables to a small number of independent factors that characterized vegetation structure on the live-trapping areas. A stepwise multiple regression analysis was then used to assess and quantify the relative importance of each of these new variables (factors) in determining the distribution and abundance of small rodents.

Because no or extremely few *P. maniculatus* were present on the Willow, Tamarack, and Black Spruce study areas, two separate factor analyses were performed; one included vegetation information from all eight study areas (to be used in further analyses with *C. gapperi* and *M. pennsylvanicus* populations in natural areas), whereas the other excluded the vegetation information from the Willow, Tamarack, and Black Spruce study areas (to be used in further analyses with *P. maniculatus* populations in natural areas). Factor analyses were run on the combined vegetation data from 1978 and 1979 using the BMDP4M computer program (Dixon and Brown 1979). Biological interpretations of the 17 habitat factors are summarized in Tables 17 and 18. Rotated factor loadings and details of the two factor analyses are summarized in Appendix 11.3.1 and Tables 50 and 51.

The relationships among the independent habitat factors and the abundance of each species of small rodent were then assessed using stepwise multiple regression (SMR) techniques. A separate SMR analysis was run for each of the three major species of small rodents within each of the two years of live-trapping using the BMDP2R computer program (Dixon and Brown 1979). Only factors with F-ratios larger than 4.0 were allowed to enter the SMR model. Because preliminary SMR analyses indicated that the variance of residuals was greater for high than for low estimates of the dependent variable (mouse abundance), cumulative CTN were transformed using the log or square root of (CTN + 1) (Cohen and Cohen 1975).

Because some trap-stations were used in more than one calculation of the CTN estimates on each study area, the actual denominator degrees of freedom for significance tests were reduced. To correct for this, the mean number of times a trap station was used on each study area was calculated and the denominator degrees of freedom was divided by the grand mean for all areas included in the analysis. Critical F-values were determined using the corrected denominator degrees of freedom.

Table 17. Description of habitat variables that characterize the 17 factors of the eight-study area factor analysis. (Rotated factor loadings are shown in Appendix 11.3, Table 50. Only variables whose factor loadings were greater than ± 0.250 are included in the descriptions. High factor loadings represent areas where a habitat variable is abundant, whereas low factor loadings represent areas where a habitat variable is rare or absent. Names assigned to each factor are used in all further discussions of the analysis.)

Factor	Name	Description of Variables
1	Aspen understory	- characterized by high stem densities and ground cover of shrubs such as *A. alnifolia*, *Lonicera* spp., *S. canadensis*, *S. albus*, and *Rosa* spp.; and low ground cover species such as *V. myrtilloides*, *L. borealis*, *L. ochroleucus*, *C. canadensis*, *A. uva-ursi*, and *G. boreale*.
2	Balsam poplar understory	- reflects the presence of high stem densities, ground cover, and vertical cover of shrubs such as *R. oxyacanthoides/hirtellum*, *R. triste*, *C. stolonifera*, *R. americanum*, *Alnus* spp., and *R. melanolasius*; high ground and vertical cover of *C. alpina*, *Equisetum* spp., *V. rugulosa*, and *G. triflorum*; the presence of moderate to high amounts of deadfall and litter; and little grass cover.
3	Black spruce forest	- represented by the presence of moderate to high stem densities of *P. mariana* and *L. laricina*; high ground and vertical cover of *L. groenlandicum*, *R. chamaemorus*, *V. vitis-idaea*, and mosses; little leaf litter; and an absence of grass cover.
4	Vertical cover	- measures the cumulative vertical cover of all plants up to a height of 1.5 m; and a thick accumulation of leaf litter.
5	Jack pine understory	- characterized by the presence of high densities and ground cover of *P. tremuloides* stems; high ground and vertical cover of *V. caespitosum*, *Cladina/Cladonia* spp., and *A. uva-ursi*; and sparse vertical cover.
6	Tamarack understory	- measures a high density of young *L. laricina*; high densities and cover of *B. glandulosa*; and moderate ground cover densities of *M. canadense*, *G. triflorum*, and *P. asarifolia*.
7	Willow-birch scrub	- represented by high stem densities and cover of *Salix* spp.; moderate stem densities and cover of *B. glandulosa* and *P. fruticosa*; and moderate ground cover densities of *R. acaulis*, *H. umbellatum*, *V. uliginosum*, and *P. palmatus*.
8	Successional cover	- characterized by moderate stem densities of *P. balsamifera*; high ground cover densities of *H. umbellatum*, *A. sibirica*, *Aster* spp. and *V. americana*; and moderate to low ground cover densities of *P. sagittatus* and *P. major*.
9	Rose understory	- reflects the presence of a moderate to high density and cover of *Rosa* spp.; and moderate to low ground cover of *Petasites* spp. and *G. boreale*.
10	Raspberry shrub	- represented by high vertical and ground cover of *R. melanolasius*.
11	Dwarf birch shrub	- characterized by low to moderate stem densities and cover of *B. glandulosa*; and high ground cover densities of *P. fruticosa*, *F. virginiana*, *V. uliginosum*.
12	*Viburnum* shrub	- represents high stem densities and ground cover of *V. trilobum* and *V. edule*; and a moderate ground cover density of leaf litter.
13	Dogwood shrub	- reflects the presence of high vertical and ground cover; and moderate stem densities of *C. stolonifera*.

continued...

Table 17. Concluded.

Factor	Name	Description of Variables
14	Grass/Sedge cover	- characterized by high vertical and ground cover densities of grasses/sedges; moderate vertical cover densities up to a height of 50 cm above ground; and a shallow layer of leaf litter.
15	Fireweed cover	- represents high vertical and ground cover densities of *E. angustifolium*.
16	Horsetail cover	- characterized by moderate to high ground cover densities of *Equisetum* spp.; and a shallow layer of leaf litter.
17	White spruce understory	- characterized by moderate densities of young *P. glauca*; moderate ground cover densities of *C. canadensis* and *L. borealis*; and low stem densities of *Rosa* spp.

Table 18. Description of habitat variables that characterize the 17 factors of the five study area factor analysis. (Rotated factor loadings are shown in Appendix 11.3, Table 54. Only variables whose factor loadings were greater than ± 0.250 are included in the descriptions. High factor scores represent areas where a habitat variable is abundant, whereas low factor loadings represent areas where a habitat variable is rare or absent. Names assigned to each factor are used in all further discussions of the analysis.)

Factor	Name	Description of Variables
1	Aspen understory	- characterized by the presence of high stem densities and/or ground cover of shrubs such as *Lonicera* spp., *A. alnifolia*, *S. canadensis*, and *S. albus*; high ground cover densities of *L. ochroleucus*, *V. myrtilloides*, *L. borealis*, and *M. canadense*; and moderate to low ground cover densities of *A. uva-ursi*, *G. boreale*, and *C. canadensis*.
2	Balsam poplar understory	- reflects high stem densities and/or cover of *R. oxyacanthoides/hirtellum*, *R. triste*, *C. stolonifera*, *R. americanum*, *Alnus* spp., and *R. melanolasius*; high ground cover of *C. alpina*, *Equisetum* spp., and *G. triflorum*; the presence of moderate levels of deadfall and leaf litter; an absence of grass or sedge ground cover, and *E. angustifolium* cover; and low stem densities of *Salix* spp.
3	Jack pine understory	- measures a presence of high stem densities and ground cover of young *P. tremuloides*; high vertical and/or ground cover densities of *Cladina/Cladonia* spp., *V. caespitosum*, *A. uva-ursi*, and *M. canadense*; an absence of *R. melanolasius*; sparse cumulative vertical cover at ground level (0 to 25 cm); and poor accumulations of leaf litter.
4	Vertical cover	- characterized by dense vertical cover up to a height of 1.5 m; and moderate to thick accumulations of leaf litter.
5	Successional cover	- represents a young successional habitat with high ground cover densities of *Aster* spp., *H. umbellatum*, *A. sibirica*, *V. americana*, *P. sagittatus*, and *Salix* spp.; moderate to low stem densities of *P. balsamifera* and *Salix* spp.; and a low ground cover density of *P. major*.
6	Tamarack forest	- measures the presence of high stem densities of *L. laricina* and *B. glandulosa*; high vertical and ground cover densities of *L. groenlandicum*; a moderately dense ground cover of moss; low vertical cover densities of *V. caespitosum*; and low ground cover densities of *V. uliginosum*.
7	Rose understory	- characterized by high densities of ground cover, vertical cover, and stems of *Rosa* spp.; and low ground cover densities of *R. pubescens*, *Petasites* spp., and *G. boreale*.
8	Raspberry shrub	- reflects the presence of moderate densities of stems, and dense ground and vertical cover of *R. melanolasius*.
9	*Viburnum* shrub	- characterized by high stem densities and ground cover densities of *V. trilobum* and *V. edule*; and moderate to low accumulations of leaf litter.
10	Dwarf birch shrub	- measures a presence of moderate stem densities, and dense ground and vertical cover of *B. glandulosa*.
11	Grass/Sedge cover	- represents a moderate to dense cover of grasses and sedges; moderately dense vertical cover from ground level up to a height of 50 cm; poor accumulation of leaf litter; and low ground cover densities of *H. umbellatum*.

continued...

Table 18. Concluded.

Factor	Name	Description of Variables
12	Dogwood shrub	- characterized by moderate stem densities, and dense ground and vertical cover of *C. stolonifera*.
13	Fireweed cover	- reflects the presence of high vertical and ground cover densities of *E. angustifolium*.
14	Black spruce ground cover	- represents a moderate to dense ground cover of *V. vitis-idaea* and *V. uliginosum*; and a moderate ground cover density of *M. canadense*.
15	*Equisetum* cover	- reflects the presence of a high ground and vertical cover density of *Equisetum* spp.
16	Black-white spruce transition	- characterized by a high ground cover density of *P. mariana*; low to moderate stem densities of *P. glauca* and *Salix* spp.; and low ground cover densities of *C. canadensis*.
17	Older successional	- represents the presence of dense vertical cover and moderate to low stem densities of *Salix* spp.; moderate to low densities of *P. balsamifera*; and low ground cover densities of *Salix* spp., *V. rugulosa*, and *G. triflorum*.

4.3.3 *Clethrionomys gapperi*--Habitat Structure Relationships

4.3.3.1 1978 analysis. Values of the two habitat factors (successional cover and the rose understory factors) were transformed to correct for non-normality by adding 4 (to make all values positive) and then taking the square root.

During the summer of 1978, 53% of the variation in the abundance of *C. gapperi* could be explained by 12 habitat factors (Appendix 11.3, Table 52). Areas characterized by high values of the balsam poplar understory, dogwood shrub cover, successional cover, raspberry shrub cover, *Viburnum* shrub cover, rose understory, and dense vertical cover factors were most often associated with higher numbers of *C. gapperi*, whereas habitats with high values of the aspen understory, willow-birch shrub cover, fireweed cover, and tamarack understory factors generally supported low numbers of *C. gapperi*.

Of the factors positively associated with the abundance of this microtine, balsam poplar understory was the most important predictor variable; 29% of the variance in numbers of *C. gapperi* was associated with this factor. Dogwood shrub cover was moderately important (5.6% of the previously unexplained variance). All remaining factors were statistically significant predictors of abundance, but each accounted for only 1 to 4% of the previously unexplained variance.

Based on the importance of these habitat factors as predictors of abundance and the direction of their relationship with abundance, how do the results of the SMR model relate to the major communities of the boreal forest? Mean factor scores for each habitat factor were calculated for the 30 vegetation samples on each study area (Appendix 11.3, Table 53). The expected number of CTN for one trap station on each study area was then predicted using the SMR equation (Appendix 11.3, Table 52) and the appropriate mean factor scores for that study area; the expected number of CTN were used as a means of quantitatively evaluating the relationships between these habitat factors and the major community types.

Based on expected numbers of CTN, balsam poplar and older successional habitats were most strongly associated with moderate to high numbers of *C. gapperi* in 1978 (Table 19). Strong positive associations of these habitats with high values of the balsam poplar understory and successional cover factors, respectively, were largely responsible for the positive correlation with the abundance of *C. gapperi*. Expected CTN on all other study areas in 1978 indicate that all other communities were less suitable habitats for this species. Subzero estimates of expected CTN on many of the study areas in 1978 suggest that CTN values used in the SMR were skewed upward (despite transformation) and consequently resulted in an underestimation of the expected CTN estimates.

4.3.3.2 1979 analysis. Only 20% of the variation in the abundance of *C. gapperi* on the eight study areas in 1979 was associated with habitat structure (Appendix 11.3; Table 54). Balsam poplar understory, aspen understory, successional cover, and *Viburnum* shrub cover all were associated with lower numbers of *C. gapperi*.

The balsam poplar understory, aspen understory, and successional cover factors were major predictor variables in 1979 (7.2, 5.6, and 4.6% of the variance was explained by these factors, respectively). *Viburnum* shrub cover was also a significant predictor variable but accounted for only 2.7% of the variance in abundance.

Expected numbers of CTN on each of the eight study areas in 1979 (Table 19) suggest that none of the six natural habitats or the two successional areas were strongly associated with high numbers of *C. gapperi*. Aspen, willow, black spruce, tamarack, and young successional habitats all were associated with approximately the same numbers of animals, whereas jack pine, balsam poplar, and older successional habitats were associated with lower numbers of animals. The apparent lack of strong associations between *C. gapperi* numbers and specific communities in 1979 suggests that habitat structure was not a major influence on *C. gapperi* abundance during this period.

Table 19. The expected number of CTN of small rodents during the summer of 1978 and 1979. (The expected CTN was derived using the appropriate SMR equation[a] for the species and year, and the mean factor scores for each predictor variable on each study area[b]. Expected mean CTN values shown are for one trap station on each area.)

Species	Year	Study Areas Jack pine	Aspen	Willow	Balsam Poplar	Poplar Creek Cutline	Black Spruce	Thirkwood Cutline	Tamarack
C. gapperi	1978	-0.15	-0.15	-0.17	0.01	0.00	-0.12	-0.17	-0.16
	1979	0.02	0.05	0.05	0.02	0.03	0.05	0.06	0.05
M. pennsylvanicus	1978	0.03	0.02	0.07	0.01	0.14	0.09	0.09	0.09
	1979	0.03	0.02	0.03	0.05	0.08	0.04	0.02	0.02
P. maniculatus	1978	0.03	0.03	-	0.12	0.03	-	0.08	-
	1979	0.10	0.14	-	0.02	0.02	-	0.04	-

[a] See Appendix 11.3, Tables 52 and 54 for *C. gapperi*, Tables 57 and 58 for *M. pennsylvanicus*, and Tables 60 and 62 for *P. maniculatus* in 1978 and 1979, respectively.

[b] See Appendix 11.3, Tables 53 and 55 for the eight-area analysis and Tables 61 and 63 for the five-area analysis in 1978 and 1979, respectively.

4.3.3.3 Inter-year comparisons of SMR models. Based on the two SMR models, the relationships in 1978 between habitat structure and the abundance of *C. gapperi* appeared to be different from the relationships in 1979; a smaller percentage of the variance in abundance was explained by habitat structure in 1979 than in 1978 (20% vs. 54%, respectively), and the number of and specific predictor variables differed between years. For example, balsam poplar understory was the most important predictor of *C. gapperi* abundance in both years, but accounted for more of the variance in abundance in 1978 than in 1979. Further balsam poplar understory was positively correlated with *C. gapperi* abundance in 1978 but was negatively correlated with abundance in 1979.

Changes in the relative magnitude of the multiple regression coefficients (R) between 1978 and 1979 could be attributed to either:

1. Changes in the specific habitat variables characterizing each habitat factor; or
2. Changes in the importance of or inclusion of different habitat factors as predictors of abundance.

Because the factor analysis of the habitat variables was performed on the combined data for 1978 and 1979, vegetation factors were identical in both years and, consequently, would not influence the SMR analyses. Changes in the importance of individual habitat factors and the inclusion of different habitat factors, however, could alter the SMR analyses in both years. These changes might be attributable to variation in the habitat affinities of a species with decreasing population densities, changes in population structure, or variation in interspecific competition.

Differences in the relationship between habitat structure and the abundance of *C. gapperi* in each year were assessed by means of a second SMR analysis of the 1979 data; in the second analysis, the 12 significant habitat factors from the 1978 analysis were used to re-evaluate the 1979 data. Overall, 25.2% of the variance in the abundance of *C. gapperi* during the summer of 1979 was accounted for by the second 'forced' SMR model (Appendix 11.3, Table 56) versus a total of 20.0% in the original 1979 SMR and 53.1% in the 1978 SMR. In the forced 1979 analysis, the four habitat factors included in the original 1979 SMR were among the most important predictor variables and accounted for 16.1% of the variance. The similarity of the two 1979 analyses suggests that although similar components of habitat structure may have influenced local abundance in both years, the relationship of *C. gapperi* numbers to overall habitat structure really were different in the two years.

4.3.4 *Microtus pennsylvanicus*--Habitat Structure Relationships

4.3.4.1 1978 analysis. Eight habitat factors explained 55% of the variation in the numbers of captures of *M. pennsylvanicus* during the summer of 1978 (Appendix 11.3, Table 57). Four factors, characterizing successional cover, *Equisetum* cover, grass/sedge cover, and black spruce forest were positively correlated with the abundance of *M. pennsylvanicus*, whereas the remaining four factors, balsam poplar understory, jack pine understory, aspen understory, and white spruce understory, were negatively correlated.

Successional cover, balsam poplar understory, and jack pine understory were the most important predictor variables of *M. pennsylvanicus* abundance, accounting for 13.7, 14.0, and 12.2%, respectively, of the variance in captures of *M. pennsylvanicus*. Aspen understory accounted for an additional 6.3%, whereas each of the remaining four habitat factors accounted for only an additional 1.1 to 3.0% of the previously unexplained variance.

Based on the expected number of CTN predicted from the SMR model and mean factor scores on each study area (see Section 4.3.3.1), older successional communities (i.e., the Poplar Creek cutline) were the most suitable habitat for *M. pennsylvanicus* (Table 19). Black spruce, tamarack, and young successional habitats were moderately suitable for this species, whereas jack pine, aspen, and balsam poplar habitats were least suitable. The strong association between older successional communities and higher numbers of *M. pennsylvanicus* was largely related to the common occurrence of vegetation components comprising the successional cover factors.

4.3.4.2 1979 analysis. Overall, 27% of the variation in the number of captures of *M. pennsylvanicus* during the summer of 1979 could be related to differences in vegetation structure (Appendix 11.3, Table 58). Five habitat factors, successional cover, grass/sedge cover, balsam poplar understory, dogwood shrub cover, and *Viburnum* shrub cover, were positively correlated with the abundance of *M. pennsylvanicus* . The remaining three factors, *Equisetum* cover, tamarack understory, and jack pine understory, were negatively correlated with the numbers of this species.

Successional cover and grass/sedge cover were the two most important predictor variables of abundance in 1979, accounting for 10.3 and 5.6%, respectively, of the variance. After these factors were taken into account, *Equisetum* cover, tamarack understory, and jack pine understory accounted for an additional 2.0 to 2.3% of the variance in captures of *M. pennsylvanicus*. The remaining habitat factors were statistically significant predictor variables but each accounted for only 1.5 to 1.7% of the previously unexplained variance.

Expected numbers of CTN suggest that older successional communities were again the most suitable habitats for *M. pennsylvanicus* (Table 19). As in 1978, the high values of the successional cover factor (the most important predictor variable) on the Poplar Creek cutline were the major determinant of the strong association of *M. pennsylvanicus* numbers with this habitat. High values of the grass/sedge cover factor (the second most important predictor variable) were also common on this area. Balsam poplar and black spruce communities were moderately suitable habitats for this species in 1979, whereas jack pine, willow, aspen, young successional, and tamarack cover types were least suitable.

4.3.4.3 Inter-year comparisons of SMR models. A second SMR analysis of the 1979 data, as described previously for *C. gapperi*, was used to assess differences between the SMR models for *M. pennsylvanicus* during 1978 and 1979. All significant predictor variables in the 1978 analysis were used to re-evaluate the 1979 data.

Responses of *M. pennsylvanicus* numbers to vegetation structure appeared to have changed between 1978 and 1979. Habitat factors significantly associated with local abundance in 1978 accounted for only 8.7% of the variance in the number of captures of *M. pennsylvanicus* in 1979 (versus 26.9% in the original 1979 SMR and 55% in the 1978 SMR) (Appendix 11.3, Table 59). The large difference in the R-square values for the two 1979 SMR analyses imply that the habitat factors associated with *M. pennsylvanicus* in 1978 were different from those in 1979. Further, the large differences between the R-square values for the 1978 and 1979 SMR imply that the relationship between *M. pennsylvanicus* abundance and habitat structure also changed between years. Notably, balsam poplar and jack pine understory were important predictor variables in 1978, whereas grass/sedge cover was a major predictor variable in 1979. Successional cover was the most important predictor variable in both years.

4.3.5 *Peromyscus maniculatus*--Habitat Structure Relationships

4.3.5.1 1978 analysis. Habitat structure accounted for 48% of the variance in the abundance of *P. maniculatus* on the five study areas during the summer of 1978 (Appendix 11.3, Table 60). Seven habitat factors, balsam poplar understory, *Equisetum* cover, dense vertical cover, jack pine understory, successional cover, aspen understory, and grass/sedge cover all were significantly related to the numbers of captures of *P. maniculatus*. The first three factors were positively correlated, whereas the last four factors were negatively correlated with the abundance of this species.

Balsam poplar understory was the most important predictor variable of *P. maniculatus* abundance in 1978; 16.8% of the total variance in abundance was attributable to this habitat factor. After taking this into account, jack pine understory and successional cover explained an additional 8.3% and 7.8% of the variance in abundance, whereas aspen understory accounted for an additional 5.5%. The remaining three factors were significant predictors of *P. maniculatus* abundance but were associated with only 2.6 to 4.3% of the variance in numbers.

Based on the expected number of CTN as predicted by the above SMR equation and the mean factor scores on each study area, balsam poplar forest was the most important habitat for *P. maniculatus* (Table 19). The strong association between this habitat and *P. maniculatus* was largely related to the common occurrence on this area of vegetation composing the balsam poplar understory factor (the most important predictor variable). The Thickwood Cutline study area (a young successional community) was also a highly suitable habitat for *P. maniculatus*; vegetation components characterizing successional cover and a lack of jack pine understory were common on this area. The remaining three community types, aspen forest, jack pine forest, and older successional areas appeared to be marginally suitable habitats for *P. maniculatus*.

4.3.5.2 1979 analysis. During the summer of 1979, seven habitat variables explained 48% of the variation in the abundance of *P. maniculatus* (Appendix 11.3, Table 62). Both jack pine and aspen understory were positively associated with the abundance of *P. maniculatus*--together these two factors accounted for 37% of the total variation in the numbers of captures. The remaining five factors, balsam poplar understory, raspberry shrub cover, grass/sedge cover, young successional growth, and *Equisetum* cover, all were negatively correlated with the abundance of *P. maniculatus*. However, each accounted for only 1.5 to 3.4% of the previously unexplained variance.

Expected numbers of CTN for *P. maniculatus* in 1979 suggest that aspen and jack pine forests were the most suitable habitats for this mouse species (Table 19). The common occurrence of vegetation characterizing the aspen understory and jack pine understory factors, respectively, on each of these areas was largely responsible for the close association of *P. maniculatus* abundance with these habitats. Young successional habitats (i.e., the Thickwood cutline) appeared to be moderately suitable, whereas balsam poplar and older successional communities were least suitable for *P. maniculatus*.

4.3.5.3 Inter-year comparisons of the SMR models. The 1978 and 1979 SMR analyses of the relationship between vegetation structure and the abundance of *P. maniculatus* accounted for almost identical proportions of the variance in abundance of *P. maniculatus* in each year (48.4% in 1978 versus 48.2% in 1979). However, the importance of some predictors changed between years. A second SMR analysis of the 1979 data was performed, using the significant predictor variables for *P. maniculatus* in 1978 to assess differences between years. The 'forced' SMR model of the 1979 data accounted for 52.5% of the variance in abundance, versus 48.2% in the original 1979 SMR and 48.4% in the 1978 SMR (Appendix 11.3, Table 64). The small differences in the R-square values of the three models indicate that the importance of the association of overall habitat structure with *P. maniculatus* numbers did not change appreciably between years. However, changes in the direction and importance of specific predictor variables between years suggest that *P. maniculatus* may have responded to different habitat components in 1978 and 1979.

4.4 DISCUSSION

Why do small rodents select specific habitat types over others? Habitat preferences probably have evolved in response to processes of natural selection; animals that inhabit marginal habitats produce fewer offspring than animals living in optimal habitats and consequently are selected against (Krebs 1978). Small populations in more marginal areas, however, likely are sustained by dispersal of animals from more suitable habitats. Three aspects of habitat selection and use were of interest in this study:

1. Which habitats were most preferred by each species of small rodent and which habitats were least used;
2. What characteristics of preferred and marginal habitats were associated with differences in the abundance and distribution of small rodents; and
3. Were characteristics of populations in these preferred habitats consistent with the suggestion that the reproductive success of populations in optimal habitats is higher than that of populations in marginal habitats?

4.4.1 Habitat Preferences and Use

Based on peak population sizes and preferences for specific tree and shrub species, balsam poplar and tamarack forest cover types were the most important habitats for *C. gapperi*. Moderate to high numbers of animals were captured on live-trapping areas in these habitats and statistically significant preferences were shown for some of the tree and shrub components of balsam poplar communities (i.e., *P. balsamifera, Rosa* spp., *Viburnum* spp., and *Alnus* spp.) and tamarack forests (i.e., *L. laricina* and *B. glandulosa*).

In contrast, successional areas and jack pine forest were marginally suitable habitats for *C. gapperi*; populations in these habitats were small and major tree and shrub species associated with these habitats were avoided (i.e., no shrub cover, *Salix* spp., *P. banksiana*, and *A. alnifolia*).

The preference of *C. gapperi* in the Athabasca region for balsam poplar or tamarack forest cover and avoidance of areas with limited tree or shrub cover (e.g., successional areas, jack pine forest, willow-birch scrub) agrees with a number of previous studies of this species. *Clethrionomys gapperi* has been shown to be associated closely with the boreal montane forest biome and is limited primarily to the more mature forest communities of this ecotone (Criddle 1932;

Williams 1955; Gunderson 1959; Hoffman 1960; Rickard 1960; Cameron 1964; Iverson et al. 1967; Miller and Getz 1972, 1977; Richens 1974; Lovejoy 1975; Kucera and Fuller 1978). Distributions within these communities appeared to be related most closely to the amount of cover provided by vegetation, debris, and litter and to the amount of available water (Connor 1953; Miller and Getz 1972, 1973; Lovejoy 1975).

Microtus pennsylvanicus in northeastern Alberta showed significant preferences for and most frequently inhabited successional areas (i.e., no tree or shrub cover). On the other hand, jack pine and black spruce habitats were only marginally suitable for this species. Both areas supported moderate to very low numbers of mice and habitats dominated by *P. mariana* were significantly avoided by *M. pennsylvanicus*.

Preferences by *M. pennsylvanicus* for successional areas, willow shrub cover, and tamarack forest are very similar to those reported by studies in other areas of Canada and the northern United States; *M. pennsylvanicus* was found to occur most commonly in moist habitats with dense grass-dominated or sedge-dominated ground cover (Findley 1951, 1954; Connor 1953; Eadie 1953; Mossman 1955; Getz 1960; Hoffman 1960; Zimmerman 1965; Iverson et al. 1967; Wrigley 1969; Grant 1971a; Hodgson 1972; Douglass 1976a). *Microtus pennsylvanicus* has also been shown to inhabit woodland areas, particularly areas comprised of open woods and grassy vegetation (Buckner 1957; Smith and Foster 1957; Clough 1964; Connor 1960; Morris 1969; Grant 1971a; Krebs and Wingate 1976; Douglass 1976a).

Peromyscus maniculatus in the Athabasca Basin were most abundant in and preferred balsam poplar forests (i.e., significant preferences for *P. balsamifera* and *Alnus* spp.). In contrast, willow-birch shrub and tamarack habitats were avoided (no captures on live-trapping areas in these habitats and an avoidance of *Salix* spp. and *B. glandulosa* shrub cover). Jack pine and black spruce forests were only marginally suitable (very low numbers of animals and an avoidance of *P. mariana* and *B. glandulosa* cover types).

As in this study, *P. maniculatus* have been shown to chiefly inhabit woodland areas, particularly mature, deciduous-coniferous forests with dense shrub understories and damp soils (Hoffman 1960; Iverson et al. 1967; Sheppe 1967; Baker 1968; Wrigley 1969; Dyke 1971; Grant 1971b; Richens 1974; Lovejoy 1975; Krebs and Wingate 1976). Detailed studies of small mammal populations in the boreal montane forest communities of the southern Yukon indicated that *P. maniculatus* was most common in closed white spruce forests with buffalo-berry understory, followed by beach ridge areas, closed white spruce forests, aspen woods, closed white spruce-aspen forest, and balsam poplar forests with buffalo-berry understory (Krebs and Wingate 1976). Moderate to low numbers of *P. maniculatus* were captured in grass-fireweed meadows, white spruce-birch forests, *Dryas drummondi* flats, closed white spruce forests with moss or willow understory, and willow scrub.

Peromyscus maniculatus is also a common resident of prairie habitats throughout most of the north-central United States (Hays 1958; Lobue and Darnell 1959; Wecker 1963; Brown 1964; Iverson et al. 1967; Beck and Vogl 1972). In addition, this species appears to readily colonize disturbed areas such as post-burn or post-logging successional areas (Williams 1955; Tevis 1956a, 1956b; Gashwiler 1959, 1969; Ahlgren 1966; Lawrence 1966; Hooven 1969; Hooven and Black 1976; Martell and Radvanyi 1976). In this study, disturbed habitats (i.e., the two cutline study areas) supported moderate numbers of *P. maniculatus* but did not appear to be as suitable as some forested areas. Recent studies of *P. maniculatus* populations in disturbed sites and in adjacent forest habitats similarly have indicated that early successional areas are poorer quality habitats than mature forest communities (Petticrew and Sadlier 1974; Lovejoy 1975; Sullivan 1979a, 1979b). Populations in disturbed communities typically undergo a rapid turnover of animals throughout the year; recruitment to disturbed areas during the late spring and summer is generally high but population sizes decline overwinter as a result of higher mortality and higher rates of emigration than in forested areas (Sullivan 1979a, 1979b).

4.4.2 Habitat Structure and Small Rodent Abundance

What characteristics of the major boreal forest communities in the Athabasca Basin were associated most often with high levels of use (or avoidance) by *C. gapperi*, *M. pennsylvanicus*, or *P. maniculatus*? In this study, multivariate statistical techniques proved useful in evaluating (1) the relationships between specific components of habitat structure and local abundances of the major small rodent populations in each year and (2) the relationship between these components and use of major habitat types.

4.4.2.1 *Clethrionomys gapperi*. Although similar habitat factors were significantly associated with *C. gapperi* abundance in 1978 and 1979, the nature of these relationships differed between years. In 1978, the overall importance of habitat structure as a predictor of abundance was twice as great as in 1979. This suggests that *C. gapperi* abundance in 1979 was influenced by some factors that were not included in the SMR analysis; these factors may have involved other aspects of habitat structure (both biotic and abiotic characteristics) or intrinsic responses (i.e., behavioural or physiological) of *C. gapperi*. The decline in numbers of *C. gapperi* and trappability between years may also have influenced the statistical associations of habitat structure and abundance in 1979.

Based on multivariate analyses described previously, *C. gapperi* in 1978 were generally more abundant in areas with dense shrub understories (comprised largely of *C. stolonifera*, *Ribes* spp., *Alnus* spp., or *R. melanolasius*), dense ground cover, and moderate to thick accumulations of litter and deadfall. In contrast, low numbers of *C. gapperi* were associated most often with areas of moderate to low accumulations of leaf litter, moderate to dense ground cover, and moderate to dense shrub cover dominated by *A. alnifolia*, *Lonicera* spp., *S. canadensis*, *S. albus*, *Rosa* spp., *Salix* spp., *B. glandulosa*, or *Viburnum* spp. The similar densities of shrub cover in both the more suitable and marginal habitat types suggest that shrub densities were not directly associated with *C. gapperi* abundance. Rather, the species composition of the shrub understory, the density of the ground cover, the accumulation of leaf litter, and the presence of deadfall were important habitat components associated with higher numbers of *C. gapperi*.

In contrast, relationships between *C. gapperi* abundance and specific components of habitat structure in 1979 were not well defined (i.e., all predictor variables were negatively correlated with *C. gapperi* abundance). Consequently, variation in local numbers of *C. gapperi* in 1979 was associated most closely with the absence rather than the presence of specific components of habitat structure. Lower numbers of *C. gapperi* were associated most often with dense shrub understory, dense ground cover, and moderate to thick accumulations of leaf litter and deadfall.

Habitat relationships of *C. gapperi* in 1978 were similar to those described by a number of other studies of small rodent habitat use. Local distributions of *C. gapperi* have been shown to reflect dense vegetation cover, deadfall, and deep accumulations of leaf litter (Williams 1955; Gunderson 1959; Miller and Getz 1972, 1973, 1977; Powell 1972). Miller and Getz (1972, 1973, 1977) found that *C. gapperi* avoided fields, clearings, and unforested areas and, in particular, found that population numbers were highly correlated with the amount of vegetation debris. Powell (1972) compared *C. gapperi* population densities in a mature forest area with those in a recent blowdown area (where deadfall was abundant) immediately adjacent to this forest and found that the density in the blowdown area was three times that in the forested area.

Available moisture also has been shown to affect the distribution of *C. gapperi* (Butsch 1954; Hoffman 1960; Miller and Getz 1972, 1973, 1977). Getz (1968) concluded from a laboratory study of water balance of *C. gapperi* that the relatively inefficient kidney of this species necessitated a high daily intake of water. As a result, the species often is restricted to low, wet areas or to areas where abundant, succulent food is available

(Miller and Getz 1972, 1973). Water availability also may have affected the distribution of *C. gapperi* in this study. Balsam poplar understory was associated closely with *C. gapperi* abundance in 1978 and was a major component of vegetation on the Balsam Poplar study area; this area was consistently damp (as evidenced by the dense growth of *Equisetum* spp. and ferns in some areas) and standing water was common after rains in 1978. Conversely, the jack pine understory factor was associated with low numbers of *C. gapperi* and was a common component on the Jack Pine study area--jack pine forests are one of the most xerophytic plant communities in the region (Stringer 1976). However, willow-birch shrub and tamarack communities were also located in poorly drained sites yet were poorly correlated with the abundance of this species. This suggests that, although water availability may be an important factor associated with *C. gapperi* distributions, it is not the only factor associated with higher numbers of this species.

Changes in population size or population structure may also have resulted in real changes in habitat use by *C. gapperi* or in apparent changes in the statistical associations of this species with habitat structure. For example, the decline in *C. gapperi* numbers between 1978 and 1979, probably contributed to the lower R^2 in 1979 SMR analyses. The lower the abundance of animals, the greater the likelihood that a larger proportion of the total variance is comprised of measurement and sampling errors, which cannot be accounted for by SMR analyses.

Changes in population sizes of *C. gapperi* or other species of small rodents may also influence interspecific competition (particularly with *M. pennsylvanicus*) and in turn may affect local distributions of *C. gapperi*. The presence of *C. gapperi* in forested areas has been shown to restrict the occurrence of *M. pennsylvanicus* (Cameron 1964; Morris 1969; Morris and Grant 1972), whereas the presence of *M. pennsylvanicus* in grassland areas can restrict *C. gapperi* to more forested areas (Grant 1969). Almost all

M. pennsylvanicus and *C. gapperi* populations declined between 1978 and 1979. However, most *M. pennsylvanicus* populations underwent much more pronounced declines than did most *C. gapperi* populations. The absence of *M. pennsylvanicus* in some habitats possibly allowed *C. gapperi* to disperse into areas from which it was excluded previously and so decreased the apparent relationship between local abundances and areas which previously had been used more intensively. Such changes in microhabitat selection by two species of microtines have been observed by Douglass (1976b) following experimental manipulations of populations in exclosures.

4.4.2.2 *Microtus pennsylvanicus*. Based on the habitat associations of the SMR analyses, *M. pennsylvanicus* in the Athabasca region in 1978 and 1979 occurred most often in areas dominated by dense successional plant cover. Areas characterized by high ground cover densities of *H. umbellatum, A. sibirica, Aster* spp., and *V. americanum*, and moderate densities of *P. balsamifera* generally supported higher numbers of *M. pennsylvanicus* than other plant associations. In 1979, *M. pennsylvanicus* were also abundant in grass/sedge communities characterized by dense growths of grasses and sedges, moderately dense vertical cover up to a height of 50 cm, and a shallow accumulation of leaf litter.

Close associations of *M. pennsylvanicus* with a number of species of grasses, sedges, and legumes similarly have been observed in other studies (Eadie 1953; Hoffman 1960; Zimmerman 1965; Hodgson 1972; M'Closkey 1975; Douglass 1976a). As in this study, Douglass (1976a) found that numbers of *M. pennsylvanicus* in boreal forest communities in the vicinity of Chick Lake, Northwest Territories, were highest in open areas, particularly those dominated by dense graminoid cover.

Distributions of *M. pennsylvanicus* also have been shown to be affected by the density of ground cover and the structure of the canopy. In this study, numbers of *M. pennsylvanicus* were highest in areas with dense canopies of either successional herbaceous plants and/or grasses and sedges. Eadie (1953) showed that areas of a grassland with high indices of mouse density had almost double the amount of ground cover (by weight) of areas with low indices of mouse density. Hodgson (1972) also found that the distribution of *M. pennsylvanicus* was significantly correlated with the amount of plant biomass and the total coverage of the herbaceous and shrub canopy--areas with a plant biomass greater than 700 g/m^2 or with herb-shrub cover greater than 85% appeared to be the most favourable habitats. Studies by Lobue and Darnell (1959), Zimmerman (1965), and Birney et al. (1976) similarly have shown that distributions of *M. pennsylvanicus* are related directly to the density of vegetation and in particular in high densities of graminoid cover.

In contrast, lower numbers of *M. pennsylvanicus* in the Athabasca Basin during 1978 commonly were associated with understory communities of balsam poplar, jack pine, aspen, and white spruce forests. In 1979, low numbers were observed most often in areas of willow-birch scrub, black spruce forest, tamarack understory, and jack pine understory. Other studies have similarly indicated that *M. pennsylvanicus* typically avoided mature forest habitats; however, it was able to and did occupy woodland areas, particulary areas comprised of open woods and grassy vegetation (Buckner 1957; Smith and Foster 1957; Clough 1964; Connor 1960; Morris 1969; Grant 1971a; Hodgson 1972; Krebs and Wingate 1976).

Comparisons of the 1978 SMR analysis with the 'forced' 1979 SMR analysis suggested that overall importance of habitat structure, as well as the importance of individual habitat factors as predictors of *M. pennsylvanicus* abundance differed between years. As discussed previously for *C. gapperi*, part of the apparent decline in the importance of habitat structure probably reflects the effects on the 1979 SMR analysis of the decline in numbers and trappability between 1978 and 1979. Changes in population sizes and structure, however, may have resulted in real differences in habitat use by this species. Studies of habitat selection and interspecific competition in small rodent communities have suggested that, although *M. pennsylvanicus* normally occupies grassland areas, density-dependent dispersal may occur into woodland areas (Morris 1969; Grant 1970, 1971a; Morris and Grant 1972). Assuming that most *M. pennsylvanicus* populations in the Athabasca Basin reached peak numbers in 1978 (Section 3), indices of habitat use during that year may reflect a broader range of habitat use as a result of such density-dependent dispersal. Indices of habitat use during the population decline in 1979 consequently may more accurately describe selection of optimal habitats in lieu of intra-specific competition for more suitable areas.

4.4.2.3 *Peromyscus maniculatus*. In 1978, high numbers of *P. maniculatus* were most common in areas with a dense shrub understory dominated by *Ribes* spp., *C. stolonifera, Alnus* spp., and *R. melanolasius*, a dense ground cover of *Equisetum* spp. and several herbs, moderate to thick accumulations of litter and deadfall, an absence of grass/sedge cover and dense vertical plant cover up to a height of 1.5 m (the highest zone measured). Preferences by *P. maniculatus* for forested areas with dense shrub and ground cover similarly have been reported by Hoffman (1960), Iverson et al. (1967), Sheppe (1967), Baker (1968), Wrigley (1969), Dyke (1971), Grant (1971b), Richens (1974), Lovejoy (1975), and Krebs and Wingate (1976). Close associations between the density and complexity of shrub understory and distributions of several different species of *Peromyscus* also have been reported by M'Closkey (1975) and Dueser and Shugart (1978, 1979).

Relationships between habitat structure and abundance of *P. maniculatus* in 1979 were almost directly opposite to the relationships in 1978. Higher numbers of *P. maniculatus* in 1979 were associated with the understory communities of aspen, jack pine, and successional habitats, whereas low numbers of this species were associated with the dense shrub understory components of balsam poplar forests. However, the overall importance of habitat structure (i.e., the cumulative R^2 for the SMR analyses) as a predictor of *P. maniculatus* abundance did not change appreciably between years. This suggests that although the association of specific components of habitat structure with abundance did change between years, the importance of habitat structure did not.

Because population sizes of *P. maniculatus* changed little between years, it is unlikely that changes in numbers were related to variation in habitat affinities. However, changes in micro-habitat selection by *P. maniculatus* may be related to changes in levels of interspecific competition with *M. pennsylvanicus* or *C. gapperi*. For example, Grant (1971b) showed that, although *P. maniculatus* commonly inhabited woodland areas, when densities in woodland areas increased, more intense intraspecific competition forced young animals into grassland areas. However, in the presence of high density *M. pennsylvanicus* populations, *P. maniculatus* was excluded totally from grassland areas. Similar relationships between *P. maniculatus* and *Microtus oregoni* populations in British Columbia were observed by Petticrew and Sadlier (1974) and Taitt (1978). Because *M. pennsylvanicus* populations in the Athabasca Basin declined sharply between 1978 and 1979, changes in the relationships between habitat structure and *P. maniculatus* abundance may have been related to changes in levels of interspecific competition between these species and the possible expansion of *P. maniculatus* into previously unexploited or marginally used habitats.

4.4.3 Demographic Indices of Habitat Quality

If habitat selection is related to the successful production of offspring, populations in preferred or commonly used habitats should be characteristic of populations with high reproductive success. If this is the case, and if all demographic and vegetation indices of habitat quality used in this study correctly approximated habitat quality, assessments of habitat quality within each habitat should be similar. Such comparisons of indices also will define more strongly the habitat affinities of each small rodent species. Six indices of habitat quality, measured in this study, were thought to be most useful in delineating habitat affinities: (1) peak MNAs, (2) expected CTNs (as predicted by the SMR analysis), (3) habitat preferences (or avoidances), (4) disperal indices, (5) reproductive success (breeding activity, pregnancy rates, and juvenile recruitment), and (6) condition.

4.4.3.1 *Clethrionomys gapperi*. Based on the six indices of habitat quality, balsam poplar habitats most closely approximated optimal habitats for *C. gapperi* (Figure 19); the population reached a high peak MNA; expected CTN was high; *Rosa* spp. was abundant in the area and was highly preferred by *C. gapperi*; dispersal was limited; reproductive success was good; and the condition of animals in this habitat (i.e., fat deposits) was above average. Aspen and jack pine forests were generally moderately well-suited for *C. gapperi*; in both cases, peak MNAs and expected CTN were small, whereas some shrub species in each habitat were preferred by *C. gapperi*, reproductive success was good, animals were in average or above-average condition, and dispersal was limited. The remaining five habitat types appeared only minimally-suitable for *C. gapperi*. Populations in successional areas were characterized by moderately high peak MNAs and expected CTNs but low reproductive success, poor condition, and high dispersal. In contrast, populations in black spruce habitats were characterized by low indices of abundance but higher indices of reproductive success and limited dispersal. Indices of habitat quality for populations in willow and tamarack communities were generally moderate, except for reproductive success and expected CTNs; both of these indices were low in both communities.

Habitat affinities of *C. gapperi* were not as well defined in 1979 as in 1978; most habitats were characterized by several high indices and one or more low indices of habitat quality (Figure 20). Indices of habitat quality in aspen, jack pine, and young successional habitats (i.e., Thickwood cutline) were more consistently moderate to high than in the remaining habitats. Most indices of habitat quality, except expected CTN and reproductive success, were also high on Balsam Poplar study areas. Overall, it appeared that jack pine, young successional, aspen, and balsam poplar were the best-suited habitats for *C. gapperi* in 1979, whereas willow, black spruce, tamarack, and older successional areas were more poorly suited.

Inter-year comparisons of habitat quality indicate that balsam poplar, aspen, and jack pine communities were consistently

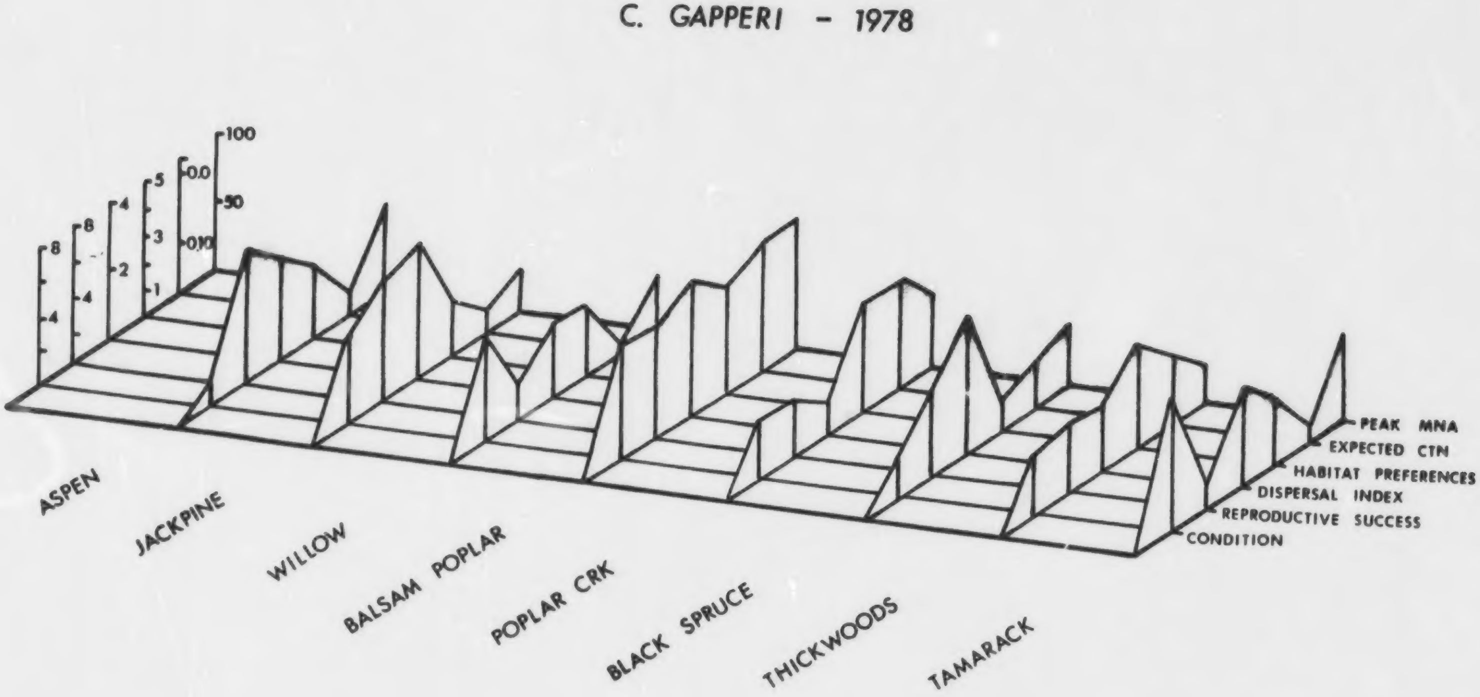


Figure 19. Habitat affinities of *C. gapperi* during June to November 1978. (Each of the indices of habitat quality was ranked as described in Appendix 11.3.2.)

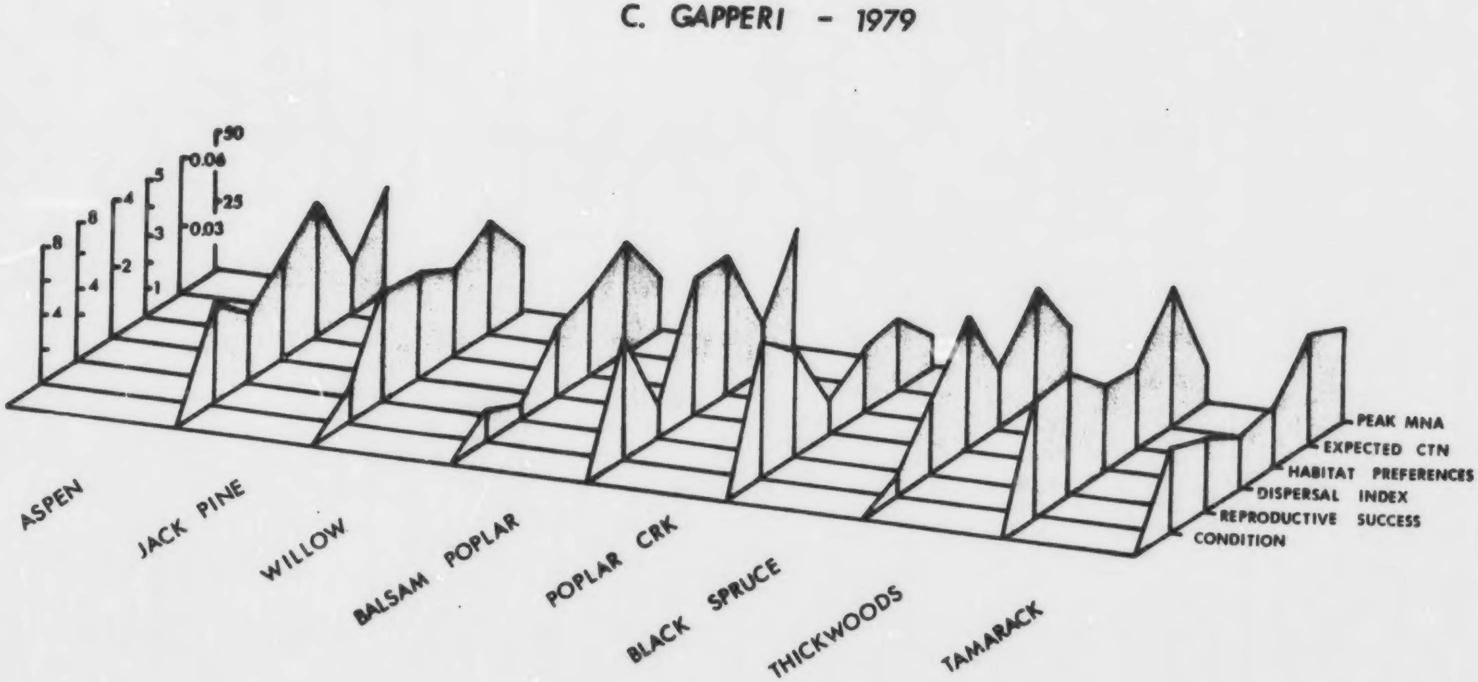


Figure 20. Habitat affinities of *C. gapperi* during May to November 1979. (Each of the indices of habitat quality was ranked as described in Appendix 11.3.2.)

the best suited habitats for *C. gapperi*. In contrast, willow shrub habitat was consistently poorly-suited for this species.

4.4.3.2 *Microtus pennsylvanicus*. Willow shrub and successional habitats were the best quality habitats for *M. pennsylvanicus* in 1978 (Figure 21). Populations in these communities were characterized by moderate to high peak MNAs and expected CTNs, significant preferences were shown for tree and/or shrub species in each habitat, dispersal was moderate to low and reproductive success was moderate to good. Tamarack and black spruce habitats were moderately well-suited, whereas aspen, jack pine, and balsam poplar forests were marginal habitats for *M. pennsylvanicus*. In particular, populations in the latter three habitats, were characterized by low indices of abundance and poor reproductive success or condition.

During 1979, older successional areas (Poplar Creek cutline) appeared to be near-optimal habitats for *M. pennsylvanicus* (Figure 22); the peak MNA and expected CTN was high, dispersal was moderate to low, reproductive success was good, and animals were in above-average condition. Indices of habitat quality in willow, balsam poplar, young successional, and tamarack communities were variable but suggested that these habitats were only moderately suitable for this microtine. Jack pine and black spruce forests were marginally suitable for *M. pennsylvanicus* (moderate to poor indices of habitat quality).

During both years of study, willow and successional communities were the best quality habitats for *M. pennsylvanicus*. The minor changes in indices of habitat quality in these habitats between 1978 and 1979 suggest that the quality of these communitites for *M. pennsylvanicus* was not altered greatly by year-to-year variations in vegetation structure.

4.4.3.3 *Peromyscus maniculatus*. During June to November 1978, balsam poplar forest and young successional areas appeared to be near-optimal habitats for *P. maniculatus* (Figure 23); peak MNAs and

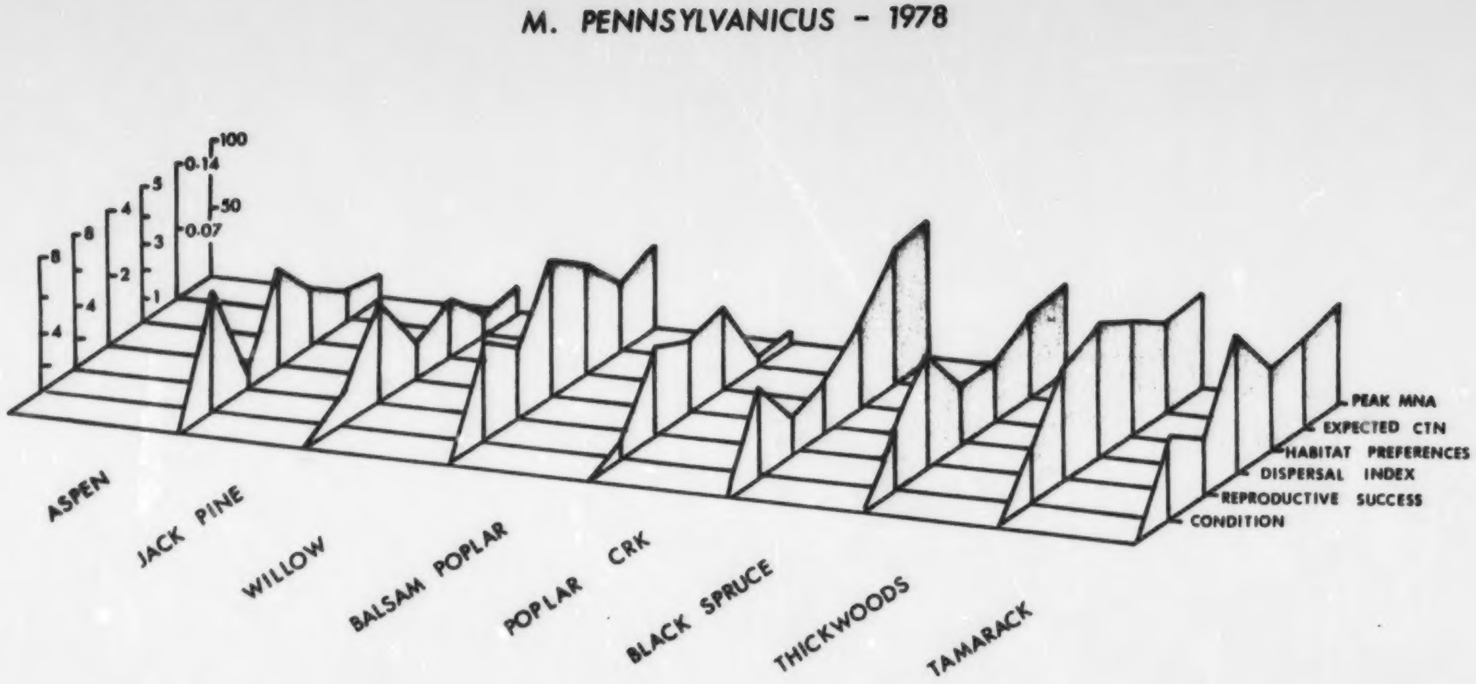


Figure 21. Habitat affinities of *M. pennsylvanicus* during June to November 1978. (Each of the indices of habitat quality was ranked as described in Appendix 11.3.2.)

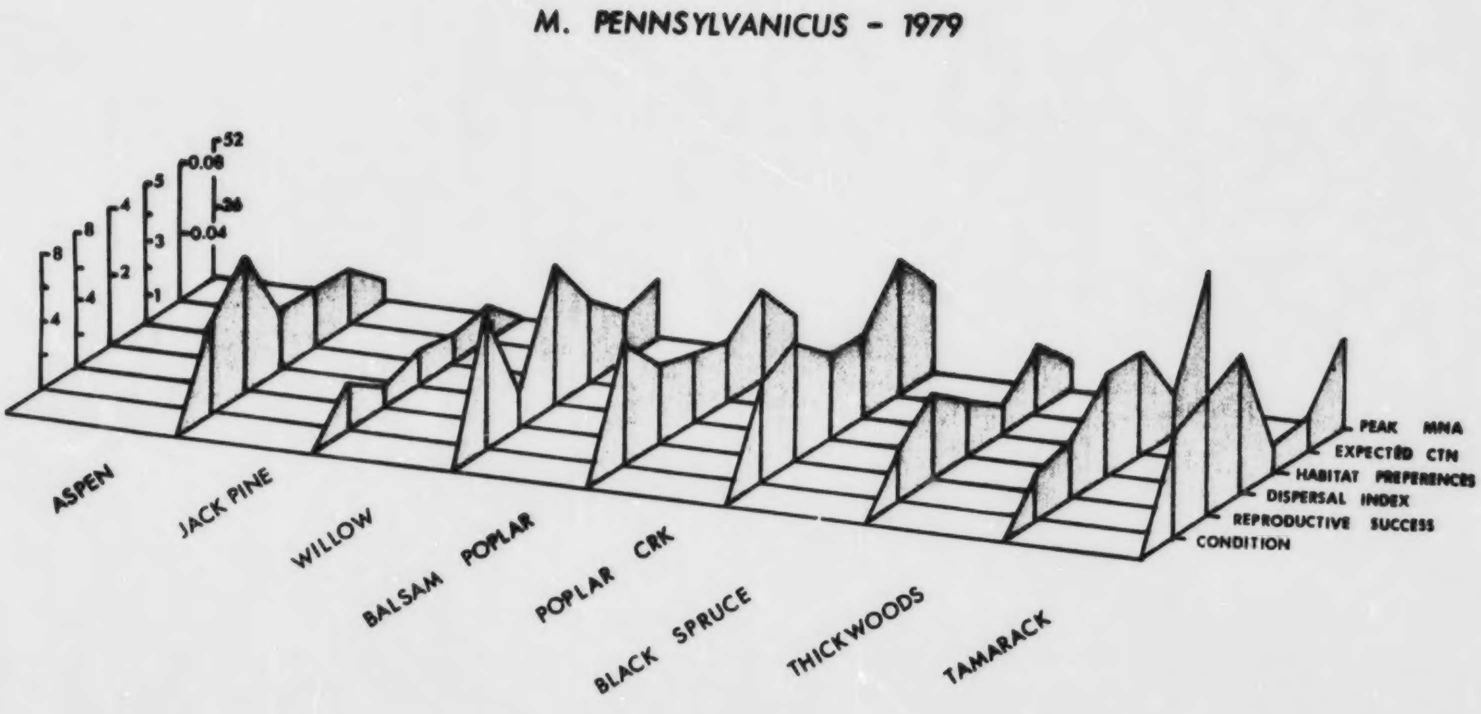
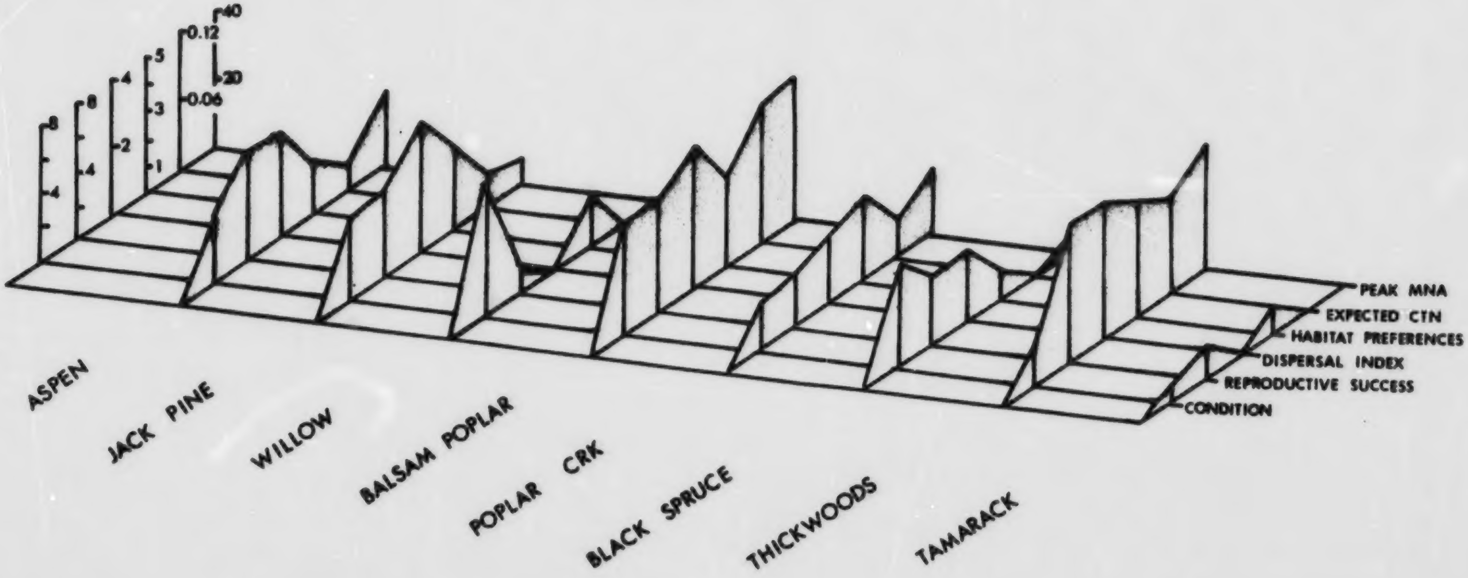


Figure 22. Habitat affinities of *M. pennsylvanicus* during May to November 1979. (Each of the indices of habitat quality was ranked as described in Appendix 11.3.2.)



P. MANICULATUS - 1978

Figure 23. Habitat affinities of *P. maniculatus* during June to November, 1978. (Each of the indices of habitat quality was ranked as described in Appendix 11.3.2.)

expected CTNs were high, some tree components of these habitats were preferred by *P. maniculatus*, dispersal was limited, reproductive success was good, and the conditions of animals (in balsam poplar forest only) were above average. Jack pine and aspen forest were moderately well-suited for this cricetid. Older successional, black spruce, and, in particular, willow shrub and tamarack communitites were marginal habitats for *P. maniculatus*; indices of abundance were low; some tree and shrub components of these communities were significantly avoided; dispersal was high; reproductive success was poor; and conditions of animals (except in the willow shrub) were below average.

Somewhat similar trends in habitat quality were apparent in 1979 (Figure 24). Balsam poplar, aspen, jack pine, and young successional communities were best-suited for *P. maniculatus*, whereas willow shrub, older successional areas, and black spruce forests were marginal habitats for this species. Tamarack forest was an extremely poor quality habitat for *P. maniculatus*; all indices of habitat quality were low.

Inter-year comparisons of habitat quality indicate that balsam poplar and young successional communities were consistently high quality habitats for *P. maniculatus*. In contrast, willow shrub, tamarack forest, and older successional communities were poor quality habitats for this species. Aspen and jack pine forests, although only moderately suitable for *P. maniculatus*, did appear to offer consistently moderate to good quality habitats for this cricetid.

4.5 CONCLUSIONS

Based on comparisons of population characteristics, population sizes, and habitat preferences, balsam poplar forest and young successional communities appeared to be the most important habitats for small rodents in the Athabasca Basin of northeastern Alberta. Balsam poplar communities were high quality habitats for *C. gapperi* and *P. maniculatus*, whereas young successional areas were near-optimal habitats for *M. pennsylvanicus* and *P. maniculatus*.

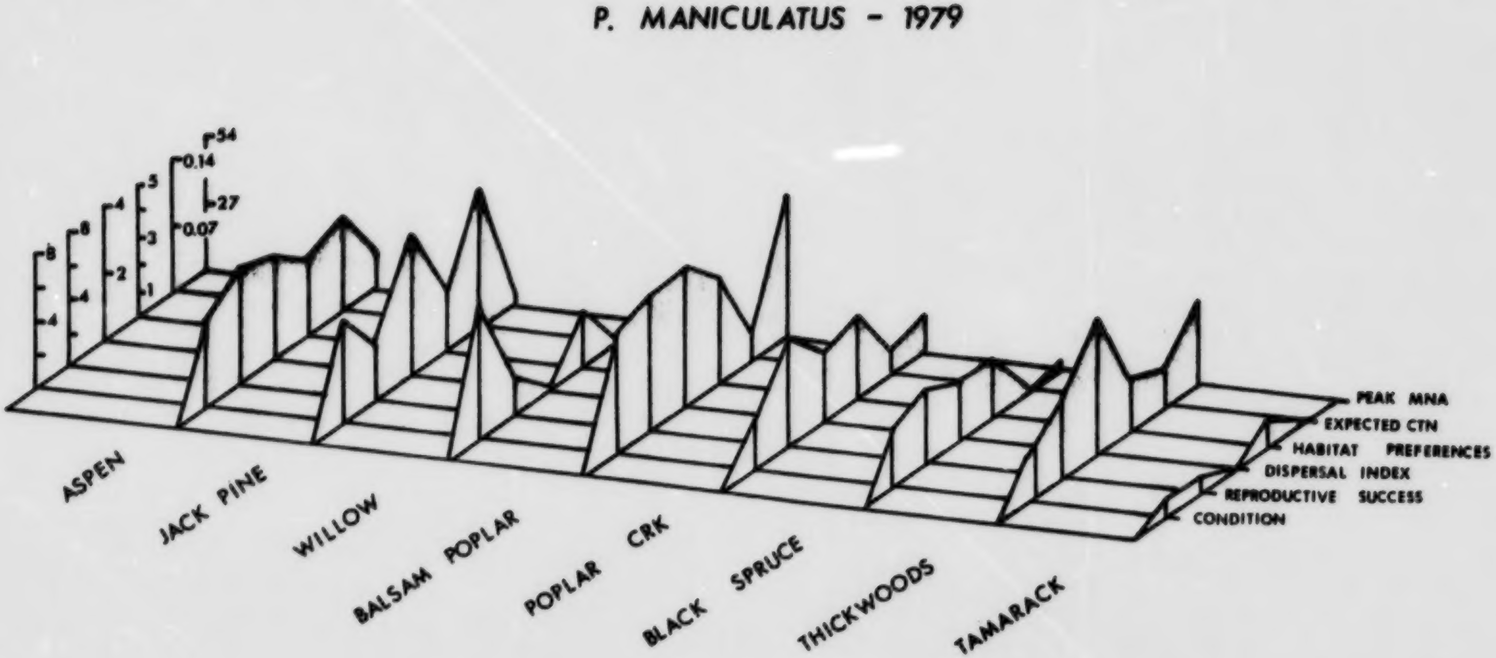


Figure 24. Habitat affinities of *P. maniculatus* during May to November, 1979. (Each of the indices of habitat quality was ranked as described in Appendix 11.3.2.)

Jack pine and aspen forests were moderately suitable habitats for small rodents. Both communities supported small to moderate numbers of *C. gapperi* and *P. maniculatus* but populations in these areas were moderately productive in relation tc populations in other communities. Neither habitat, however, was well-suited for *M. pennsylvanicus*.

Older successional and willow communities were high quality habitats only for *M. pennsylvanicus*. Habitat use by and population characteristics of *C. gapperi* and *P. maniculatus* suggested that these communities were not important habitats for these species.

Black spruce and tamarack forests appeared to be the least suitable habitats for small rodents in the Athabasca Basin. Both forest communities were poorly suited for *C. gapperi* and *P. maniculatus* and were only moderately adequate for *M. pennsylvanicus*.

Because of the importance of balsam poplar, aspen, and jack pine communities on small rodents in the AOSERP study area, impacts of oil sands developments to small rodent populations can be best minimized by avoiding destruction of these major community types. However, disturbance of vegetation in some areas may promote seral growth and succession to willow-dominated communities, which in turn may actually benefit some small rodents. Although current mining practices in the oil sands area destroy both the vegetation cover and mineral soil (and so retards or inhibits natural succession), properly designed reclamation and afforestation programs that mimic natural succession could minimize impacts of oil sands developments to *M. pennsylvanicus* and *P. maniculatus*. However, loss of large areas of mature mixed-wood or deciduous communities and the subsequent long period of regeneration resulting from disturbance of the mineral soil, could severely affect the numbers and productivity of *C. gapperi* populations.

5. SMALL RODENTS: SEASONAL DIETARY CHANGES

Assessments of seasonal changes in the diets of small rodents are an important component of baseline studies; information on dietary composition is useful in determinations of resource utilization and may also be of value in future evaluations of the mobilization and transfer of toxic chemicals. Analysis of the stomach contents of the three major species of small rodents in the Athabasca area, *Clethrionomys gapperi*, *Microtus pennsylvanicus*, and *Peromyscus maniculatus*, were undertaken primarily to identify seasonal changes in food habits and to supplement information on habitat use (Section 4).

5.1 METHODS

Food habits were determined by microhistological examination of stomach contents of mice captured during the snap-trap census program in 1979. Stomachs were removed from all specimens during the standard autopsy procedure (Section 3) and were preserved in formalin.

Analyses of stomach contents were performed by the Composition Analysis Laboratory of the Range Science Department, Colorado State University, following the methods described by Sparks and Malechek (1968). One slide was prepared for each stomach and twenty fields were systematically evaluated on each slide.

An analysis of at least 15 stomachs for each species in each monthly block of trapping was attempted. If more than 15 specimens were available, stomachs for analysis were selected randomly. If less than 15 specimens were available, all specimens were included.

In most cases, plant fragments were identified only to genus. Fragments of woody-stemmed plants, however, were also identified as leaf or bark tissue because of the implications of the consumption of woody-stemmed plants by small mammals in the assessment of small rodent damage to trees and shrubs. Because of limitations in the microhistological analysis, such identification of specific plant tissues was feasible only for tree or shrub species that exceeded a percent relative density of 10% within a sample. Insect parts were all classified as one group.

5.2 RESULTS

5.2.1 *Clethrionomys gapperi*: Seasonal Food Habits

Based on both the average percent relative density of plant fragments and the frequency of occurrence in the stomach contents, lichens were the major component of the diet of *C. gapperi* during the period of May to November 1979 (Table 20). Mycorrhiza, arthropods, *Salix* spp., *Equisetum* spp., mushrooms, and seeds were also important components of the *C. gapperi* diet throughout most of the sampling period.

Lichens were the most abundant food item in stomachs in May, October, and November and were the second most abundant food item in all other sampling months except September. Mycorrhiza, arthropods, *Salix* spp., and mushrooms were only seasonally important. *Salix* spp. were a major dietary item in June, arthropods were common foods in July, mushrooms were moderately abundant in stomachs in August, and mycorrhiza were commonly consumed in August and, particularly, in September. Such seasonal variation likely reflects changes in the availability of these items during the spring and summer periods. *Equisetum* spp. and seeds were consumed in moderate to low quantities throughout most of the May to November period. A number of other plant species were present in low quantities (Table 20) but were consumed by only a few animals (i.e., a low percent occurrence).

Four species of woody-stemmed plants, *Populus* spp., *Prunus* spp., *Salix* spp., and *Shepherdia canadensis* were present in the stomach contents of *C. gapperi* captured in 1979 (Table 21). Leaf tissue of *Prunus* spp. and *Populus* spp. were consumed in small amounts by single specimens of *C. gapperi* in June and July, respectively. Bark tissue and small amounts of leaf tissue of *S. canadensis* were present in two stomach samples in May. *Salix* spp. were consumed throughout the May to November period; bark tissue being consumed

Table 20. Percent relative density of discerned plant fragments in *C. gapperi* stomach samples. (The mean percent relative density, range of values, and percent occurrence for each plant species or group are shown. Sample sizes for each month are indicated.)

	May N=29			June N=13 (15)[a]			July N=25		
Species	$\bar{x}$ % Rel. Den.	Range	% Occ.	$\bar{x}$ % Rel. Den.	Range	% Occ.	$\bar{x}$ % Rel. Den.	Range	% Occ.
Agropyron spp.									
Aralia spp.	1.88	0-43.96	10.3	0.11	0-1.44	7.6			
Arctostaphylos uva-ursi	0.23	0-6.68	3.4						
Aster spp.	0.09	0-2.69	3.4	0.62	0-8.00	7.6			
Astragalus spp.	0.09	0-2.50	3.4						
Carex spp.							0.49	0-10.82	8.00
Compositae	0.05	0-1.41	3.4						
Cornus spp.	1.17	0-34.06	3.4						
Empetrum nigrum	0.05	0-1.44	3.4						
Epilobium angustifolia				0.30	0-3.90	7.6	0.05	0-1.27	4.0
Equisetum spp.	7.33	0-75.12	34.48	8.07	0-46.48	38.5	5.22	0-87.87	12.0
Galium spp.							0.17	0-4.24	4.0
Impatiens spp.							0.06	0-1.38	4.0
Legumes				0.94	0-12.26	7.6			
Lichens	61.25	0-100.0	82.76	26.23	0-92.11	53.8	17.63	0-98.56	68.0
Medicago sativa									
Mosses	0.91	0-22.62	8.80	0.27	0-3.56	7.6	0.05	0-1.36	4.0
Mushrooms	0.21	0-4.44	6.90				4.30	0-84.11	24.0
Mycorrhiza	3.98	0-83.29	10.34	9.35	0-92.96	15.4	7.60	0-88.27	16.0
Petasites spp.	0.45	0-10.54	6.90	0.33	0-4.32	7.6			
Pinus banksiana	0.14	0-4.19	3.45						
Plantago spp.	0.13	0-2.39	6.90	0.58	0-5.15	15.4			
Poa spp.									
Pollen							2.52	0-63.02	4.0
Populus spp.				0.94	0-12.18	7.6			
Potentilla spp. *Geum* spp.	0.97	0-20.1	10.34				0.11	0-2.81	4.0
Prunus spp.							0.75	0-18.65	4.0
Ribes spp.	2.27	0-65.82	3.45				0.69	0-17.34	4.0
Rosa spp.							0.17	0-2.78	8.0
Salix spp.	4.12	0-98.56	27.59	40.09	0-94.85	69.2	1.61	0-18.23	28.0
Seeds	2.81	0-29.36	27.59				6.36	0-98.56	36.0
Shepherdia canadensis	0.78	0-12.18	6.90				0.08	0-2.05	4.0
Symphoricarpos albus	0.92	0-26.76	3.45	0.10	0-1.36	7.6	0.51	0-11.33	8.0
Taraxacum officinale							3.28	0-78.03	12.0
Trifolium spp.							1.73	0-43.2	4.0
Vaccinium spp.							0.53	0-13.28	4.0
Viburnum spp.	0.10	0-2.92	3.45						
Viola spp.	0.26	0-7.57	3.45						
Unknown forbes	2.04	0-30.81	10.34				0.06	0-1.38	4.0
Arthropods	7.17	0-75.64	58.62	12.07	0-66.91	46.2	46.03	0-100.0	76.0

continued...

Table 20. Continued.

Species	August N=17 (21)			September N=11 (12)			October N=15		
	x̄ % Rel. Den.	Range	% Occ.	x̄ % Rel. Den.	Range	% Occ.	x̄ % Rel. Den.	Range	% Occ.
Agropyron spp.									
Aralia spp.									
Arctostaphylos uva-ursi									
Aster spp.									
Astragalus spp.									
Carex spp.	1.69	0-28.7	5.9						
Compositae							0.15	0-2.22	6.7
Cornus spp.							1.66	0-16.56	13.3
Empetrum nigrum									
Epilobium angustifolia	0.61	0-6.92	11.8						
Equisetum spp.	6.63	0-61.04	29.4	1.91	0-19.11	10.0	3.67	0-41.45	20.0
Galium spp.									
Impatiens spp.									
Legumes									
Lichens	23.19	0-100.0	47.1	0.90	0-9.02	10.0	48.08	0-100.0	80.0
Medicago sativa									
Mosses									
Mushrooms	22.47	0-97.08	47.1	11.41	0-100.0	30.0	0.09	0-1.40	6.7
Mycorrhiza	27.55	0-100.0	35.3	68.42	0-100.0	90.0	16.08	0-98.50	46.7
Petasites spp.							0.83	0-12.45	6.7
Pinus banksiana									
Plantago spp.									
Poa spp.							0.27	0-4.05	6.7
Pollen							6.39	0-95.80	6.7
Populus spp.				1.13	0-11.33	10.0			
Potentilla spp. *Geum* spp.							0.75	0-8.96	13.3
Prunus spp.				0.90	0-9.02	10.0			
Ribes spp.				5.56	0-55.6	10.0			
Rosa spp.									
Salix spp.	2.88	0-18.89	41.2	4.76	0-23.09	40.0	11.49	0-87.82	60.0
Seeds	6.84	0-100.0	23.5				6.18	0-40.37	53.3
Shepherdia canadensis									
Symphoricarpos albus									
Taraxacum officinale									
Trifolium spp.							0.19	0-2.83	6.7
Vaccinium spp.									
Viburnum spp.									
Viola spp.									
Unknown forbes	5.65	0-48.44	23.5						
Arthropods	2.49	0-16.33	35.3	5.01	0-19.11	60.0	4.17	0-27.84	40.0

continued...

Table 20. Concluded.

	November N=28 (33)		
Species	$\bar{x}$ % Rel. Den.	Range	% Occ.
Agropyron spp.	0.12	0-3.39	3.6
Aralia spp.			
Arctostaphylos uva-ursi			
Aster spp.			
Astragalus spp.			
Carex spp.			
Compositae			
Cornus spp.	0.40	0-7.77	10.7
Empetrum nigrum			
Epilobium angustifolia	0.13	0-3.67	3.6
Equisetum spp.	4.84	0-98.56	25.0
Galium spp.			
Impatiens spp.			
Legumes	1.13	0-31.74	3.6
Lichens	60.45	0-100.0	89.3
Medicago sativa	0.12	0-3.39	3.6
Mosses			
Mushrooms	1.59	0-34.12	10.7
Mycorrhiza	1.57	0-44.05	3.4
Petasites spp.			
Pinus banksiana	0.21	0-3.39	7.1
Plantago spp.			
Poa spp,			
Pollen			
Populus spp.			
Potentilla spp. *Geum* spp.			
Prunus spp.			
Ribes spp.	0.05	0-1.40	3.6
Rosa spp.			
Salix spp.	14.79	0-92.37	64.3
Seeds	4.52	0-97.08	28.6
Shepherdia canadensis			
Symphoricarpos albus			
Taraxacum officinale			
Trifolium spp.			
Vaccinium spp.	1.83	0-42.43	10.7
Viburnum spp.			
Viola spp.	3.73	0-95.56	7.1
Unknown forbes			
Arthropods	4.52	0-79.48	21.4

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[a] Sample sizes in parentheses include samples which were unsuitable for microhistological analyses (e.g., tissue decomposed). Means shown include only readable samples.

Table 21. Percentages of leaf and bark tissue of woody-stemmed species consumed by *C. gapperi*.

Month	*Populus* spp.			*Prunus* spp.			*Salix* spp.			*S. canadensis*		
	% Bark	% Leaf	N	% Bark	% Leaf	N	% Bark	% Leaf	N	% Bark	% Leaf	N
May	-	-	0	-	-	0	90	10	1	85.4 ± 5.3	14.6 ± 5.3	2
June	0.0	12.2	1	-	-	0	99.5 ± 1.4	0.5 ± 1.4	9	-	-	0
July	-	-	0	0.0	18.7	1	0.0	100.0	1	-	-	0
August	-	-	0	-	-	0	0.0	100.0 ± 0.0	2	-	-	0
September	-	-	0	-	-	0	0.0	100.0 ± 0.0	2	-	-	0
October	-	-	0	-	0	0	100.0 ± 0.0	0.0	3	-	-	0
November	-	-	0	-	-	0	100.0 ± 0.0	0.0	11	-	-	0

mainly during the early spring and fall and leaf tissue being consumed primarily during the summer (Table 21).

5.2.2 *Microtus pennsylvanicus*: Seasonal Food Habits

Microtus pennsylvanicus populations declined sharply in most habitats in the Athabasca region in 1979 (Section 3). As a result, few animals were captured during the snap-trap census program and few samples were available for stomach analyses. Seasonal changes in diet consequently are based on few samples and may not adequately reflect normal feeding habits of this species.

Mycorrhiza and *Carex* spp. were important food items, both in quantity and in frequency of occurrence, throughout most of the sampling period (Table 22). Arthropods, *Salix* spp., moss, and *Equisetum* spp. were present seasonally in small amounts. Graminoids (*Agropyron* spp., *Agrostis scabra, Calamagrostis* spp., *Carex* spp., *Glyceria* spp., and unknown grasses) comprised a major portion (21.5 to 95.8%) of the stomach contents in May, July, October, and November.

Only one woody-stemmed species, *Salix* spp., was present in the *M. pennsylvanicus* stomachs analyzed. *Salix* spp. was consumed in very small amounts in all months except September. Because the amounts consumed were small, it was not possible to determine what types of tissue were most commonly eaten.

5.2.3 *Peromyscus maniculatus*: Seasonal Food Habits

Arthropods were the primary food item of *P. maniculatus* during all of the sample months (Table 23). Arthropods comprised from 42.7 to 92.9% of the stomach contents and were present in almost all stomach samples during all months (from 77.8 to 100% of the samples). *Salix* spp., mycorrhiza, and lichens also were seasonally important; *Salix* spp. were most commonly consumed in August and November, mycorrhiza were moderately abundant in July, and lichens were a common food item in September. Seeds from a variety of plant species (not identified in the laboratory analysis) were present in small amounts during all months.

Table 22. Percent relative density of discerned plant fragments in *M. pennsylvanicus* stomach samples. (The mean percent relative density, range of values, and percent occurrence for each plant species or group are shown. Sub-totals are also shown for all graminoids. Sample sizes for each month are indicated. No animals were captured in June.)

	May N=7 (8)[a]			July N=6			August N=2		
Species	$\bar{x}$ % Rel. Den.	Range	% Occ.	$\bar{x}$ % Rel. Den.	Range	% Occ.	$\bar{x}$ % Rel. Den.	Range	% Occ.
Agropyron spp.	0.42	0-2.91	14.3						
Agrostis scabra				0.86	0-5.13	16.7			
Calamagrostis spp.				0.44	0-2.63	16.7			
Carex spp.	20.68	0-98.56	57.1	42.14	0-98.56	50.0	4.07	0-8.13	0.5
Compositae	0.35	0-2.44	14.3						
Equisetum spp.	12.63	0-88.4	14.3				35.90	2.46-69.35	1.0
Galium spp.				0.88	0-3.47	33.3			
Glyceria spp.									
Lichens	0.35	0-2.44	14.3				14.33	0-28.65	0.5
Medicago sativa	11.81	0-78.61	29.6	2.75	0-16.47	16.7			
Mosses	8.36	0-34.01	57.1	6.0	0-34.56	33.3			
Mushrooms							7.20	0-14.39	0.5
Mycorrhiza	14.51	0-87.47	42.9	32.30	0-80.38	50.0	37.27	8.13-66.43	1.0
Petasites spp.	1.03	0-7.19	14.3						
Poa spp.	0.42	0-2.91	14.3	4.81	0-17.83	33.3			
Salix spp.	0.44	0-3.11	14.3	0.42	0-2.50	16.3	1.23	0-2.46	0.5
Seeds	0.35	0-2.44	14.3						
Symphoricarpos albus	0.42	0-2.92	14.3						
Taraxacum officinale	15.79	0-76.56	28.6						
Trifolium spp.				8.96	0-53.81	16.7			
Unknown forbes	9.13	0-34.86	28.6						
Unknown grasses									
Arthropods	3.31	0-13.68	28.6	0.44	0-2.63	16.7			
Graminoids	21.52			48.25			4.07		

continued...

Table 22. Concluded.

Species	September N=1 x̄ % Rel. Den.	Range	% Occ.	October N=6 (7) x̄ % Rel. Den.	Range	% Occ.	November N=1 x̄ % Rel. Den.	Range	% Occ.
Agropyron spp.									
Agrostis scabra									
Calamagrostis spp.									
Carex spp.				70.12	10.96-98.56	1.0			
Compositae									
Equisetum spp.				0.49	0-2.92	16.7			
Galium spp.									
Glyceria spp.				25.37	0-89.04	66.7			
Lichens									
Medicago sativa									
Mosses				1.50	0-5.80	33.3			
Mushrooms									
Mycorrhiza	18.65			0.24	0-1.44	16.7			
Petasites spp.									
Poa spp.									
Salix spp.				0.97	0-5.80	16.7	2.13		
Seeds	3.32								
Symphoricarpos albus									
Taraxacum officinale									
Trifolium spp.									
Unknown forbes									
Unknown grasses							95.74		
Arthropods	78.03			1.31	0-3.22	0.50	2.13		
Graminoids	0.0			95.49			95.74		

[a] Sample sizes in parentheses include samples which were unavailable for microhistological analyses (e.g., tissue decomposed). Means shown include only readable samples.

Table 23. Percent relative density of discerned plant fragments in *P. maniculatus* stomach samples. (The mean percent relative density, range of values, and percent occurrence for each plant species or group are shown. Sample sizes for each month are indicated.)

Species	May N=11			June N=9 (10)^a			July N=11		
	x̄ % Rel. Den.	Range	% Occ.	x̄ % Rel. Den.	Range	% Occ.	x̄ % Rel. Den.	Range	% Occ.
Amelanchier spp.									
Astragalus spp.									
Calamagrostis spp.				0.45	0-4.15	11.1			
Carex spp.									
Chenopodium spp.									
Cornus spp.									
Epilobium angustifolia									
Equisetum spp.				0.42	0-3.82	11.1	0.15	0-1.68	9.1
Glyceria spp.									
Legumes									
Lichens	0.19	0-2.13	9.1	0.51	0-4.61	11.1	1.17	0-10.42	18.1
Medicago sativa									
Mosses	1.11	0-12.18	9.1	4.58	0-41.34	11.1			
Mushrooms				0.39	0-3.52	11.1			
Mycorrhiza	1.70	0-12.18	27.3	8.64	0-66.67	22.2	20.65	0-95.72	63.6
Petasites spp.									
Pinus banksiana							0.30	0-3.29	9.1
Plantago spp.									
Prunus spp.									
Ribes spp.									
Rubus spp.									
Salix spp.				12.93	0-50.-0	55.6	1.05	0-5.13	27.3
Seeds	4.13	0-39.49	18.2	5.78	0-44.54	33.3	0.23	0-2.50	9.1
Shepherdia canadensis				0.70	0-6.33	11.1			
Stellaria longifolia				0.39	0-3.52	11.1			
Symphoricarpos albus									
Trifolium spp.									
Viola spp.									
Unknown forbes									
Unknown grasses				0.16	0-1.68	11.1			
Arthropods	92.87	0-100.0	100.0	64.59	0-100.0	100.0	76.45	0-100.0	100.0

continued...

Table 23. Continued.

	August N=18			September N=8 (9)			October N=18		
Species	$\bar{x}$ % Rel. Den.	Range	% Occ.	$\bar{x}$ % Rel. Den.	Range	% Occ.	$\bar{x}$ % Rel. Den.	Range	% Occ.
Amelanchier spp.							0.19	0-3.48	5.6
Astragalus spp.									
Calamagrostis spp.									
Carex spp.							0.10	0-3.48	5.6
Chenopodium spp.				0.36	0-2.84	12.5	0.19	0-3.48	5.6
Cornus spp.							2.74	0-34.67	27.8
Epilobium angustifolia									
Equisetum spp.									
Glyceria spp.	0.17	0-3.09	5.6						
Legumes									
Lichens				27.94	0-89.46	87.5	0.19	0-3.49	5.6
Medicago sativa							0.12	0-2.13	5.6
Mosses									
Mushrooms									
Mycorrhiza	10.13	0-72.11	55.6	8.83	0-66.47	37.5	0.30	0-4.06	11.1
Petasites spp.									
Pinus banksiana									
Plantago spp.							5.24	0-94.24	5.6
Prunus spp.									
Ribes spp.				0.38	0-3.07	12.5			
Rubus spp.	2.87	0-51.64	5.6						
Salix spp.	26.18	0-95.62	72.2	9.93	0-55.58	62.5	11.45	0-87.17	66.7
Seeds	0.83	0-8.33	16.7	0.17	0-1.32	12.5	4.23	0-40.46	33.3
Shepherdia canadensis				0.44	0-3.52	12.5	0.19	0-3.49	5.6
Stellaria longifolia									
Symphoricarpos albus	0.14	0-2.50	5.6						
Trifolium spp.	0.37	0-6.60	5.6						
Viola sp.	0.14	0-2.50	5.6						
Unknown forbes	3.83	0-51.82	11.1						
Unknown grasses							0.40	0-7.15	5.6
Arthropods	55.34	0-100.0	88.9	51.95	22.81-98.56	1.0	74.46	4.38-100.0	1.0

continued...

Table 23. Concluded.

Species	November N=9 (11) $\bar{x}$ % Rel. Den.	 Range	 % Occ.
Amelanchier spp.			
Astragalus spp.	2.93	0-26.35	11.1
Calamagrostis spp.			
Carex spp.			
Chenopodium spp.			
Cornus spp.	2.25	0-16.49	22.2
Epilobium angustifolia	0.89	0-8.05	11.1
Equisetum spp.			
Glyceria spp.			
Legumes	1.51	0-12.01	22.2
Lichens			
Medicago sativa			
Mosses			
Mushrooms			
Mycorrhiza			
Petasites spp.	0.42	0-3.78	11.1
Pinus banksiana			
Plantago spp.			
Prunus spp.	4.71	0-42.40	11.1
Ribes spp.	9.09	0-78.03	22.2
Rubus spp.			
Salix spp.	32.92	0-93.33	55.6
Seeds	1.83	0-16.44	11.1
Shepherdia canadensis			
Stellaria longifolia			
Symphoricarpos albus			
Trifolium spp.			
Viola spp.			
Unknown forbes	0.42	0-3.79	11.1
Unknown grasses	0.37	0-3.32	11.1
Arthropods	42.66	0-100.0	77.8

[a] Sample sizes in parentheses include samples which were unavailable for microhistological analyses (e.g., tissue decomposed). Means shown include only readable samples.

Three species of woody-stemmed plants, *Pinus banksiana*, *Prunus* spp., and *Salix* spp., were present in the stomach samples of *P. maniculatus*. *Pinus banksiana* and *Prunus* spp. were consumed in very small amounts and were present in only a few individual samples (Table 23). In contrast, *Salix* spp. were consumed in small to moderate amounts from June to November. During June, bark tissue was eaten most commonly [an average of 99.4% of *Salix* spp. tissue present was bark (N = 4)]. In contrast, only leaf tissues were present in samples collected in July (N=9). Both leaf and bark tissues were eaten in September (bark: 65.8%; leaf: 34.2%; N = 2) and October (bark: 46.1%; leaf: 53.9%; N = 3), whereas only bark tissue was consumed in November (N = 5).

5.3 DISCUSSION

Microhistological analyses of stomach contents of *C. gapperi*, *M. pennsylvanicus*, and *P. maniculatus* in the Athabasca region are useful primarily in providing qualitative assessments of seasonal dietary changes. Quantitative evaluations of diets (estimates of percent relative density) may not accurately represent natural variation in diets of small rodents in this study because of: (1) the small sample sizes for each species of rodent in each monthly block of trapping; (2) effects of seasonal variation in diets and seasonal availability of some items; and (3) errors associated with differential digestibility and subsequent identification of various plant and arthropod tissues.

Dietary analyses ideally should include assessments of habitat effects. However, because of the small sample sizes for all three small rodent species in this study, inter-habitat differences in diets were not quantitatively evaluated nor were quantitative analysis of inter-habitat differences in the consumption of bark attempted.

5.3.1 *Clethrionomys gapperi*

As in this study, *C. gapperi* has been shown to be an omnivore feeding largely on forbs, shrubs, berries, and fungi (Criddle 1932; Hamilton 1941; Connor 1953; Whitaker 1962; Fisher 1968; Dyke 1971). Food habits, however, are seaonally variable and largely reflect both seasonal and annual availability. For example, in years of poor fruit production, mushrooms and lichens become increasingly more important in the diet of this small rodent in the Northwest Territories (Dyke 1971). Microhistological analyses of stomach contents of *C. gapperi*, captured in the Athabasca region during May to November 1979, similarly indicated that the diet of this species was seasonally variable although some species such as lichens and mycorrhiza were staple foods throughout the sampling period.

Dyke (1971) found that *C. gapperi* were largely frugivorous during the spring and summer--overwintered berries were staple items in the spring diet and as a variety of berries (e.g., *S. canadensis*, *Fragaria* spp., *Rubus* spp.) became available in early summer, these were also consumed. Leaves of *S. canadensis, A. uva-ursi, P. tremuloides*, and mosses were also important in the diet in May and June. Lichens, mycorrhiza, arthropods, *Equisetum* spp., and *Salix* spp. were all important components of the spring diet of *C. gapperi* in the Athabasca Basin. Leaves of *Salix* spp. were a particularly important food species during June. The greater dependence of *C. gapperi* on lichens and fungi (mycorrhiza) observed in this study is similar to dietary studies by Whitaker (1962), Williams and Finney (1964), and Fisher (1968)--all found that *C. gapperi* consumed considerable amounts of fungi (up to 38% of the diet by volume) during the summer period. Arthropods were a more important food item of *C. gapperi* in this study than reported for other populations in previous studies (Fisher 1968; Dyke 1971). As reported by Dyke (1971), mushrooms also constituted a major proportion of the diet of *C. gapperi* in this study during August and September.

During the late fall and winter, *C. gapperi* has been shown to depend largely on overwintering fruits of some shrubs (e.g., *Rosa* spp., *S. canadensis, Vaccinium* spp.), lichens, remaining green vegetation, and twigs, buds, and bark of trees and shrubs (Criddle 1932; Hamilton 1941; Dyke 1971; Zemanek 1972). Late fall diets of *C. gapperi* in the Athabasca region closely approximated diets reported by these studies.

Assuming that feeding habits influence habitat use, how do dietary components of *C. gapperi* relate to habitat use in the Athabasca region? Lichens, mycorrhiza, arthropods, *Salix* spp., and *Equisetum* spp. were the most important constituents of the diet (by percent relative density). Based on peak population sizes, demography, habitat preferences, and responses to habitat structure, balsam poplar, aspen, and jack pine forests were the most important habitats for this species (Section 4.4.3.1). Although information on vegetation composition collected during this study is insufficient for estimating the availabilities of the major dietary components, descriptions of the major vegetation communities of the AOSERP study area (Stringer 1976) suggest that lichens were abundant in tamarack, aspen, and black spruce forests. *Salix* spp. were moderately abundant in the Willow, Tamarack, Aspen, and Poplar Creek Cutline study areas (Section 7.), whereas *Equisetum* spp. were moderately to very abundant in the Balsam Poplar study area. Habitat use by *C. gapperi* consequently may partially reflect the availabilities of commonly consumed foods but more detailed information on the availabilities of major food species are required.

Bark consumption by *C. gapperi* in the Athabasca region during the period of May to November 1979 was limited--bark of *S. canadensis* and *Salix* spp. were consumed during the late spring and the late summer and fall, respectively. This agrees closely with reports of an increased dependence by *C. gapperi* on twigs, buds, and bark of a number of deciduous tree and shrub species during the winter months (Criddle 1932; Hamilton 1941; Dyke 1971; Zemanek 1972).

5.3.2 *Microtus pennsylvanicus*

Microtus pennsylvanicus is largely herbivorous, feeding predominantly on grasses, sedges, and to a lesser extent on forbs throughout the year (Bailey 1924; Hamilton 1940; Jameson 1955; Thompson 1965; Zimmerman 1965). Graminoids were similarly an important food item of *M. pennsylvanicus* in the Athabasca region during the summer and early fall. Forbes such as *M. sativa, Trifolium* spp., and *T. officinale* were also seasonally important dietary components of *M. pennsylvanicus* in this study, particularly during the early summer. Seasonal use and preferences for similar forbs have been reported by Bailey (1924), Thompson (1965), and Zimmerman (1965). As in this study, Bailey (1924) and Zimmerman (1965) found that *M. pennsylvanicus* consumed insects and fungi during some seasons. However, mycorrhiza were a more important food item of *M. pennsylvanicus* in the Athabasca region than previously reported for this species in other areas. Assuming that mycorrhiza are more abundant in forested habitats than in grassland communities (Maser et al. 1978; Maser et al. 1979), the increased use of mycorrhiza by *M. pennsylvanicus* in the Athabasca region may be a result of the increased availability of mycorrhiza in habitats used by *M. pennsylvanicus* in this region, as opposed to the availability of mycorrhiza in grassland habitats (most dietary studies of *M. pennsylvanicus* have been based on populations from predominantly grassland communitites.

Based on relative percent densities, mycorrhiza, *Carex* spp., arthropods, *Salix* spp. and mosses were the major dietary components of *M. pennsylvanicus* in the Athabasca region. Comparisons of these dietary components with habitat use suggest that feeding habits and habitat use are at least partially related. Successional habitats with moderate to dense grass and shrub cover were the most important habitats for *M. pennsylvanicus* in this study--tamarack and willow habitats were moderately important (Section 4.4.3.2). No information was available on the distribution and abundance of mycorrhiza in these habitats, but *Carex* spp. were abundant in successional communities and in tamarack and willow habitats (Stringer 1976). Arthropods were most abundant [based on estimates of biomass (g)·m^2] in fens, disturbed (=successional) areas, and tamarack forest (Ryan and Hilchie 1980). *Salix* spp. occurred commonly in willow, aspen, tamarack, and older successional areas (Section 7.3), whereas mosses were abundant in tamarack forests (Stringer 1976).

Consumption of bark by *M. pennsylvanicus* was expected to be high in relation to other small ordent species--voles of the genus *Microtus* are considered to be one of the major small rodent pest species in North American and Europe responsible for severe damage to young trees in orchards and reforestation programs (Bailey 1924; Littlefield et al. 1946; Jokela and Lorenz 1959; Buckner 1970; Hansson 1971; Larsson 1975; Radvanyi 1978). However, stomach contents of *M. pennsylvanicus* from natural habitats in the Athabasca region contained only one species of woody-stemmed plant; small amounts of *Salix* spp. were consumed throughout the year. The limited occurrence of woody-stemmed plants in the diet of this species probably reflects the sampling season. Consumption of bark by *Microtus* spp. is supposedly highest during periods of food scarcity, particularly during the winter and early spring (Bailey 1924; Zimmerman 1965; Hansson 1971, 1975). Stomach samples collected during the May to November period consequently may not have included samples from periods when bark consumption is believed to be highest.

5.3.3 *Peromyscus maniculatus*

Food habits of *P. maniculatus* can best be described as opportunistic and omnivorous (Jameson 1952, 1955). Regular seasonal shifts in diet, as observed in this study, are typical of this species (Jameson 1952; Williams 1959; Dyke 1971). Variations in the quality and quantity of food in different habitats also have been shown to affect the composition of the diet. For example, Dyke (1971) found that *P. maniculatus* populations in the Northwest Territories depended on overwintering fruits during the winter but, in years of fruit crop failures, readily utilized insects. Local food shortages also appeared to be overcome by more extensive foraging excursions (Stickel 1960; Dyke 1971).

Peromyscus maniculatus in the Athabasca region, like this species in a number of other areas, are largely dependent on arthropods during the late spring (Jameson 1952; Williams 1959; Brown 1964; Gashwiler 1969; Dyke 1971). Dyke (1971) found that arthropods made up at least 90% of the diet in late May to July of each year. Berries, fruits, and seeds of grasses, shrubs, and trees are also used as they become available and gradually comprise more of the diet in the late summer and early fall (Hamilton 1941; Jameson 1952; Brown 1964; Frischknecht 1964; Whitaker 1966; Gashwiler 1969; Dyke 1971; this study). *Peromyscus maniculatus* in the Athabasca region also consumed moderate amounts of leaves of *Salix* spp. in August, September, and October; a similar consumption of deciduous leaves during the late summer was reported by Jameson (1952). Fungi when abundant may also form a major part of the diet--Williams and Finney (1964) found that 8 to 92% of the diet of *P. maniculatus* in Wyoming and Colorado was made up of the fungi *Endogone*. Consumption of fungi (mycorrhiza) by *P. maniculatus* in northeastern Alberta was common during July to September and has similarly been reported by Jameson (1952), Dowding (1955), Bakerspigel (1958), Whitaker (1962), Dyke (1971), and Maser et al. (1979).

Dyke (1971) showed that both the quantity and quality of food consumed by *P. maniculatus* varied significantly among habitats, suggesting that habitat selection by this cricetine may partially reflect availability and quality of preferred foods. *Peromyscus maniculatus* in the Athabasca region most commonly consumed arthropods, *Salix* spp., mycorrhiza, seeds, and lichens. Several indices of habitat use and quality suggested that balsam poplar forest, aspen forest, and successional communities were the most suitable habitats for *P. maniculatus* in the Athabasca region. During 1979, estimates of arthropod biomass ($g \cdot m^2$) were highest in fens, disturbed areas, tamarack forest, and deciduous shrub-wetland habitats (Ryan and Hilchie 1980). *Salix* spp. were most abundant (based on stem densities in 1979; Section 7.2.1) in willow, aspen, tamarack, and older successional areas, whereas lichens were most abundant in tamarack, aspen, and black spruce forests (Stringer 1976). No information was available on the distribution and abundance of mycorrhiza or seeds. The lower abundance of preferred foods in habitats most commonly used by *P. maniculatus* suggests that habitat selection by this species is not greatly influenced by the availability of preferred foods.

Peromyscus maniculatus commonly consume seeds and fruit of trees and shrubs (Jameson 1952; Williams 1959; Baker 1968; Gashwiler 1969; Drickhamer 1970; Dyke 1971; Everett et al. 1978) and have also been reported to occasionally consume needles of some conifers during periods of deep snow (Jameson 1952). Consumption of tree or shrub bark, as reported in this study, has not previously been reported for this cricetine. *Salix* spp. were the only species of tree or shrub from which bark was consumed; however, it is not known if this is a special case or if bark of other species may be eaten as well. Bark consumption was highest during June and November, suggesting that girdling by this species (like *C. gapperi* and *M. pennsylvanicus*) may be most common during the late fall, winter, and early spring.

Because *P. maniculatus* was not previously known to consume bark, this mouse species was not believed to be responsible for girdling damage to trees or shrubs. Rather, it was considered a major pest species because of its consumption of tree seed used in programs of reforestation by artificial seeding (see Section 7). Consumption of moderate amounts of bark of *Salix* spp. by *P. maniculatus*, however, indicates that this species is responsible for some girdling of at least one shrub species. Further investigations of diets of *P. maniculatus* in northeastern Alberta, particularly during the winter months, are required to more adequately evaluate bark consumption by this cricetine and may result in modifications to current concepts of controlling girdling damage by small rodents (see Green 1978 for a review).

6. SNOWSHOE HARES

The snowshoe hare (*Lepus americanus*) is an integral component of the small mammal community within the boreal forest, both as a herbivore and as a major prey species of several furbearers. Snowshoe hare populations undergo cyclic fluctuations in abundance every 8 to 11 years (Keith 1963; Keith and Windberg 1978) and browsing of woody vegetation during peak years is often severe (MacLulich 1937; Aldous and Aldous 1944; Cook and Robesen 1945; Trapp 1962; Grange 1965; Wolff 1978; Pease et al. 1979). Snowshoe hares are also an important prey species for a number of raptors and mammals, particularly lynx (*Lynx canadensis*). Lynx are dependent upon snowshoe hares for a major portion of their diet and changes in lynx population sizes typically reflect changes in the abundance of snowshoe hares (Keith 1963; Nellis and Keith 1968; Nellis et al. 1972; Brand et al. 1976; Brand and Keith 1979). Disturbances of snowshoe hare populations resulting from oil sands developments consequently may not only directly affect this species but may also result in changes in numbers of some predators and in vegetation composition and productivity.

The major objectives of this study were to assess the demography of and habitat use by snowshoe hares in several major plant communities of the boreal forest. Such information will provide both a data base for future comparisons with post-disturbance states and information necessary for evaluations of probable impacts of development and formulation of mitigative measures. Although a baseline study of snowshoe hares should include data on the cyclic characteristics of this species, given the short duration of this study relative to the 10 year population cycle, no specific attempt has been made to evaluate cyclic phenomena in the study populations.

6.1 SPECIFIC METHODS

6.1.1 Live-trapping Techniques

Snowshoe hares were live-trapped using techniques similar to those described by Keith et al. (1968). All study areas were trapped once every 2 wk from 30 June to 13 November 1978 and once every 3 wk from 13 May to 2 December 1979.

Each study area was 5.7 ha in size[1] and consisted of a 8 x 10 grid of trapping stations at 30 m intervals. One Tomahawk rabbit trap (single door) was placed on a well-defined runway (if possible) within a 5 m radius of alternate trap stations. Alfalfa hay or fresh clover was used as bait. All traps were prebaited (traps were locked open on both ends) for 2 wk prior to commencing live-trapping in 1978. Traps were arranged so that, during one trapping period, traps on even-numbered rows were set at the even-numbered stations, and traps on odd-numbered rows were set at the odd-numbered stations. Traps were moved between trapping periods so that, during the following trapping periods, traps on even-numbered rows were set at odd-numbered stations and traps on odd-numbered rows were set at odd-numbered stations and traps on odd-numbered rows were set at even-numbered stations. Traps were locked open between trapping periods.

Each trapping period consisted of 3 d of live-trapping. On the first day, all traps were set in the afternoon. All traps were checked and reset the following morning. On the third day, all traps were checked and locked open until the next trapping period.

Snowshoe hares were also trapped 28 February to 7 March 1979 and 22 to 31 January 1980. Each winter trapping period consisted of 5 d of live-trapping. On the first day, all traps were set in the afternoon. Over the next 2 d, all traps were checked and reset each morning. Following the second trap check, traps were moved (as described previously for between trapping periods) and set. All traps were checked and reset each morning for another two days.

Newly captured snowshoe hares were tagged with a #3 monel metal ear tag (National Band and Tag Company). The tag number, species, trap location, sex, breeding condition, weight, age [based on genital morphology (Trapp 1962)], and the number of attached ticks were recorded for each animal captured.

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[1] Partial flooding of the SH-balsam poplar grid in 1978, resulting from the damming of an old river channel by beaver, effectively reduced the trapping grid to a size of 5.0 ha (an 8 x 9 station trapping grid).

6.1.2 Vegetation Analyses

Vegetation analyses were conducted on each of the snowshoe hare live-trapping plots during the period of 30 June to 2 July 1979. Habitat availability was estimated by recording the three most dominant tree, shrub, and ground cover species, the percent coverage of each of the three ground cover species, and the density of the forest canopy in the vicinity of each trap station. The three most dominant species of trees and shrubs, respectively, were determined for the area within a 5 m radius of each station; species of trees and shrubs were ranked according to the percent coverage of the sampling area (based on the projected area of the canopy). For each of the three most dominant ground cover species (e.g., herbs, forbs, grasses, sedges, and mosses) an estimate of the percent coverage of the area within a 1 m radius of each trap station was obtained using a Braun-Blanquet cover scale (Kershaw 1966). An estimate of canopy density (cumulative percent coverage of all tree species) was recorded based on a scale of 1 to 4 (1 = canopy density 0% to <25% coverage; 2 = 25% to <50%; 3 = 50% to <75%; 4 = 75% to 100%).

6.2 SNOWSHOE HARE DEMOGRAPHY

An intensive live-trapping program was used to assess the demography of *L. americanus* in representative habitat types of the AOSERP study area. During each trapping period, a complete enumeration of the snowshoe hare population on each study area was attempted. Based on the number of snowshoe hares captured in each trapping period, the minimum number known to be alive (MNA) (Chitty and Phipps 1966) was used as a biased estimate of population size (see Section 3.2.1.1).

6.2.1 Trappability

The trappability of *L. americanus* on each of the four study areas was used to assess the reliability of the MNA estimates of population size (see Section 3.2.1.1). Minimum unweighted trappabilities (Boonstra and Krebs 1978) were calculated for each population for the summer period (30 June to 20 September 1978; 16 May to 20 September 1979) and for the fall period (21 September to 17 November 1978; 21 September to 29 November 1979).

In 1978, estimates of trappability for all study populations always exceeded 50% (Table 24)--MNA estimates consequently should underestimate the trappable population size by acceptably small amounts. In 1979, only trappabilities on the Balsam Poplar and Black Spruce study areas during the summer and on the Aspen study area during the fall exceeded 50%. Trappabilities in all other cases in 1979 were low and do not provide acceptable estimates of population sizes. These MNA estimates will be considered as underestimates throughout the remainder of this report.

6.2.2 Changes in Population Size

MNA estimates of population size for snowshoe hares on the four study areas are shown in Figures 25 to 28. In 1978, snowshoe hares were most abundant on the Black Spruce study area. Moderate numbers were present on the Balsam Poplar study area and low numbers were present on both the Aspen and Jack Pine study areas. In 1979, snowshoe hares were again most abundant in black spruce and balsam poplar cover types, whereas numbers were low in jack pine and aspen habitats (estimates on the Jack Pine and Aspen study areas are probably underestimates because of low trappabilities). Within the Balsam Poplar and Jack Pine study areas, snowshoe hares were more abundant in 1979 than in 1978 (despite poor trappability on the latter study area). In contrast, the number of snowshoe hares on the Aspen and Black Spruce study areas changed little between 1978 and 1979.

Table 24. Seasonal estimates of minimum unweighted trappability (MUT) of *L. americanus*.

	1978				1979			
	Summer		Fall		Summer		Fall	
Grid	MUT	N	MUT	N	MUT	N	MUT	N
Jack Pine	58.3	8	69.1	7	13.3	9	22.2	9
Aspen	61.1	9	60.0	5	40.8	10	66.7	3
Balsam Poplar	68.0	14	89.0	15	53.0	16	25.0	24
Black Spruce	70.4	38	79.1	30	53.7	22	43.9	22

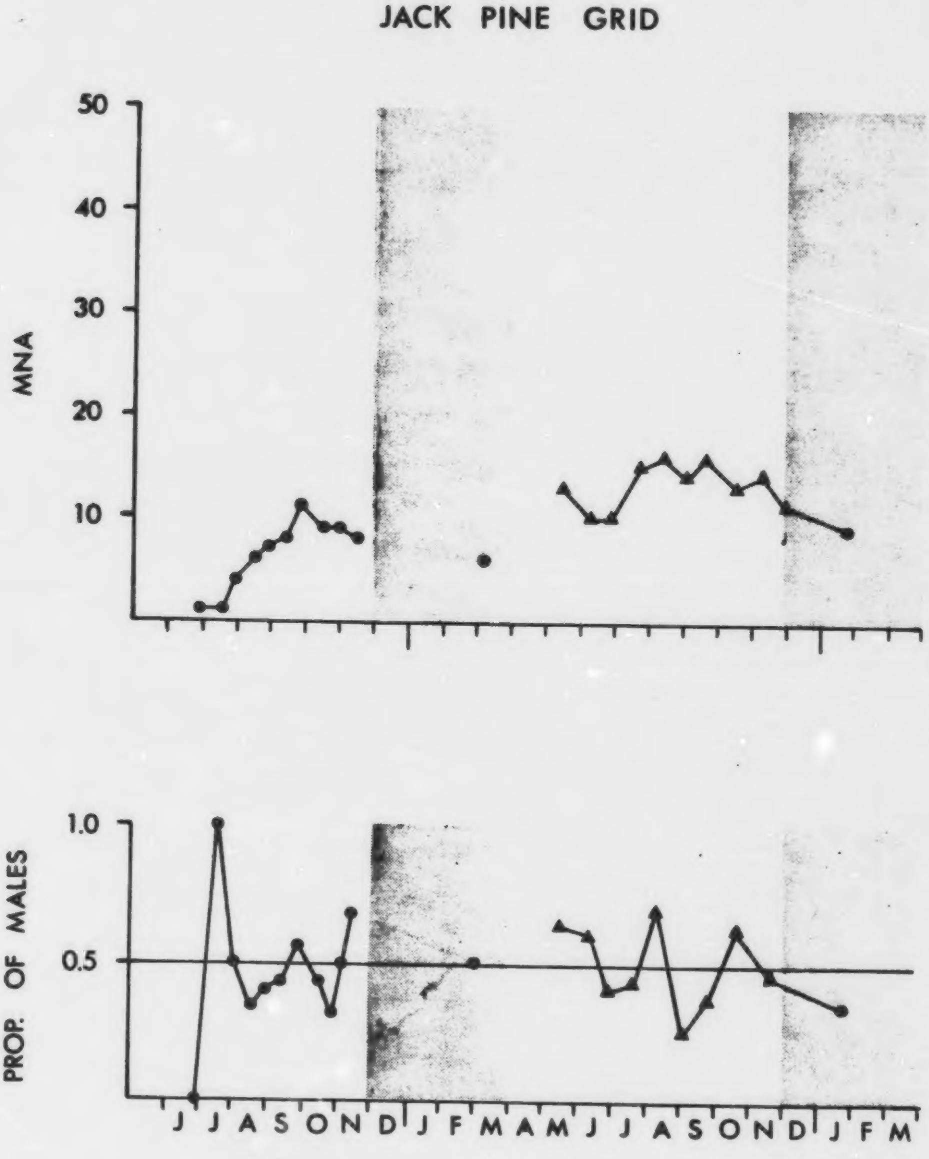

Figure 25. The MNA and sex ratios of *L. americanus* on the Jack Pine study area. (Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size. The winter periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

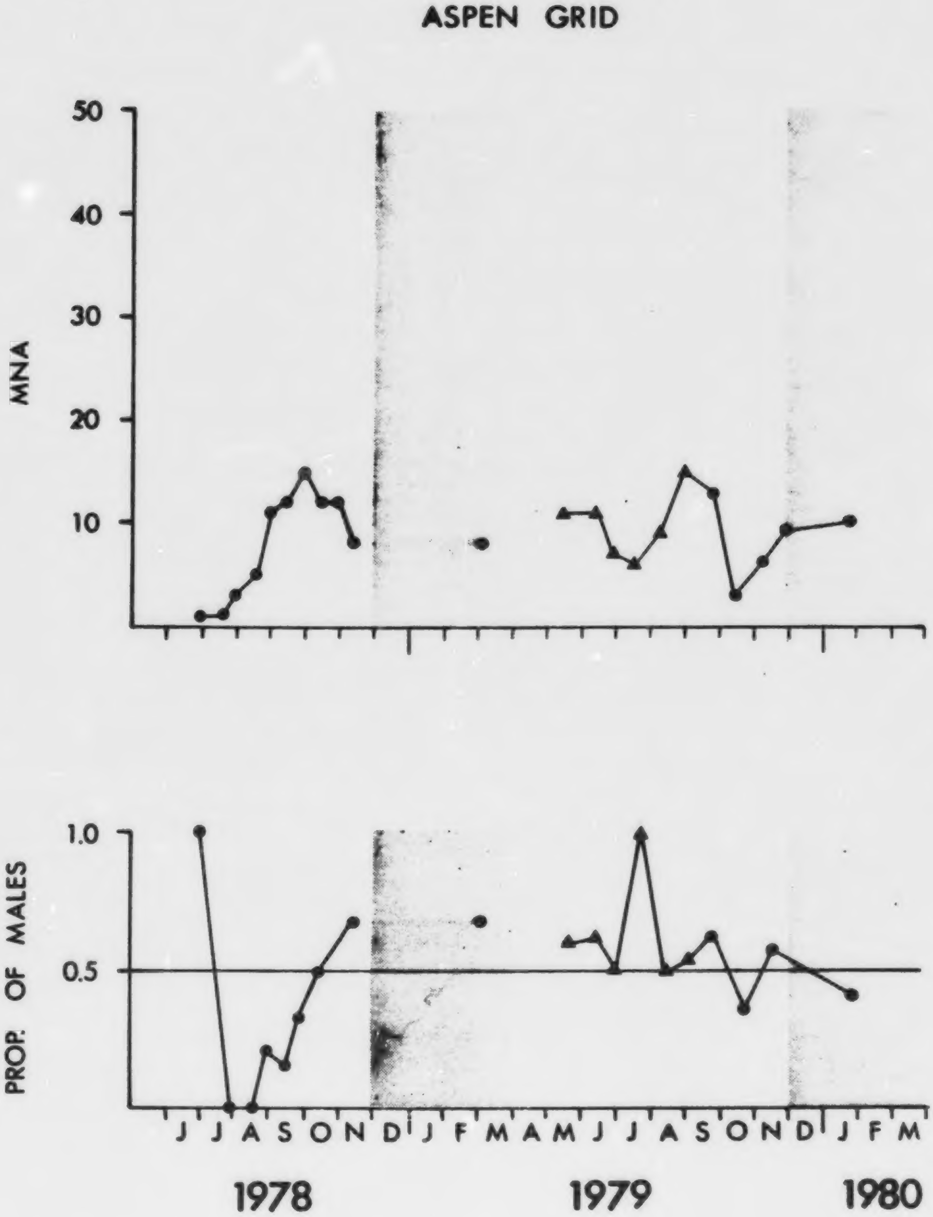

Figure 26. The MNA and sex ratios of *L. americanus* on the Aspen study area. (Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size. The winter periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

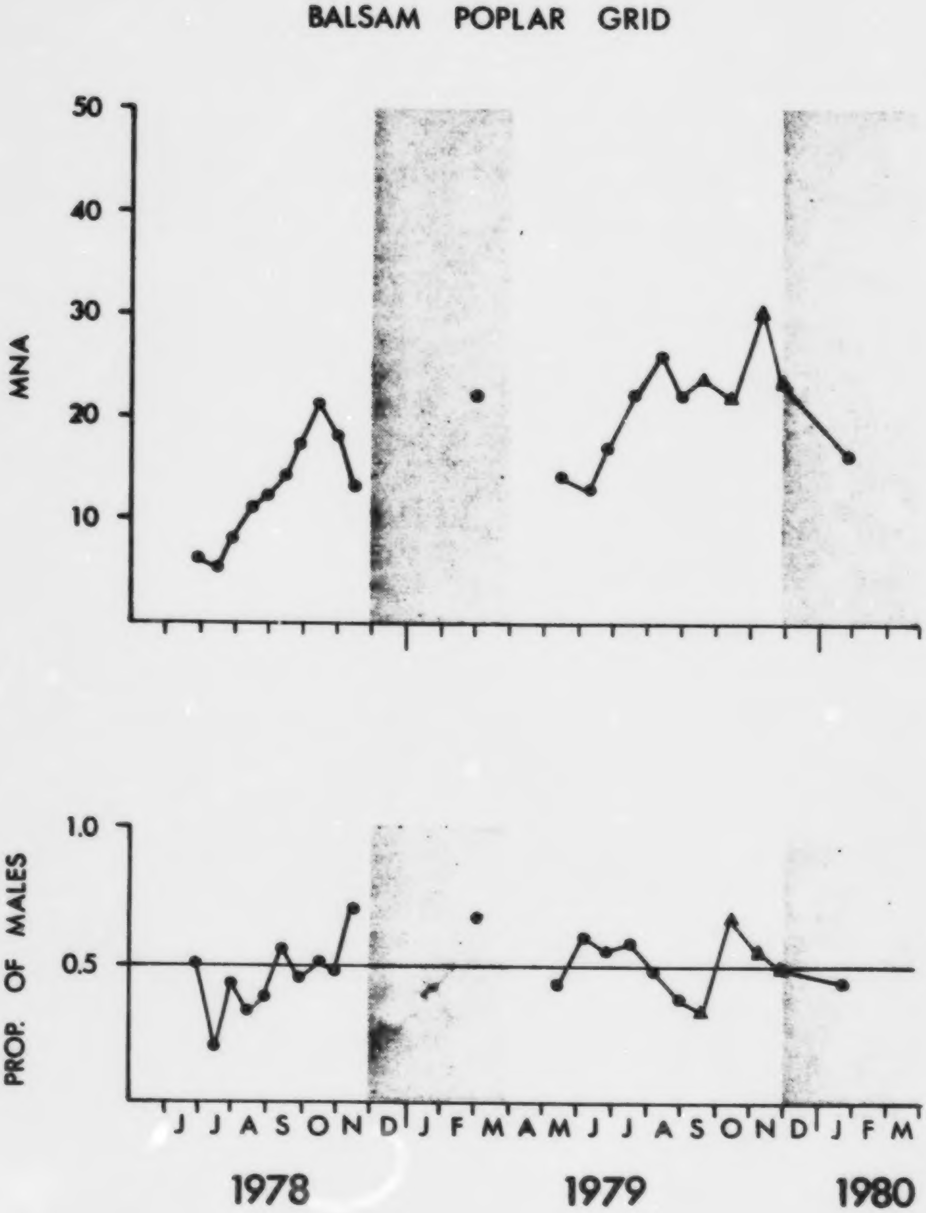

Figure 27. The MNA and sex ratios of *L. americanus* on the Balsam Poplar study area. (Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size. The winter periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

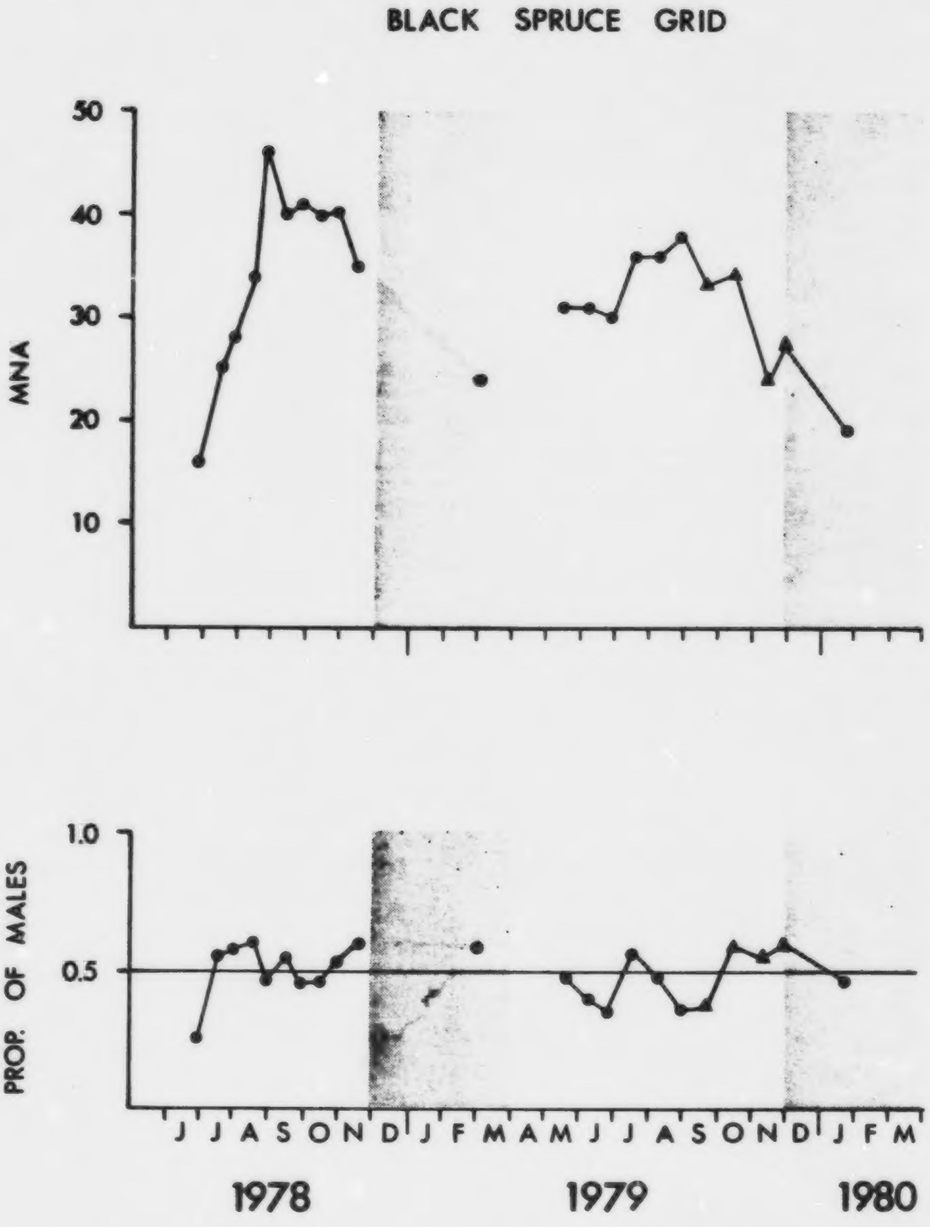

Figure 28. The MNA and sex ratios of *L. americanus* on the Black Spruce study area. (Triangles indicate that trappabilities were less than 50% and MNA estimates likely underestimate the real trappable population size. The winter periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

6.2.3 Survival and Recruitment

Changes in the numbers of snowshoe hares within a habitat are a result of population losses (mortality and emigration) and recruitment (births and immigration). Seasonal survival and recruitment rates were determined for the summer (1 July to 20 September 1978, and 16 May to 20 September 1979), fall (21 September to 9 November 1978, and 21 September to 9 November 1979), and winter (10 November 1978 to 15 May 1979, and 10 November 1979 to 25 January 1980) periods using multiple regression analyses with 'dummy' variables (Fairbairn 1977a) as described previously for small rodents (Section 3.3). Effects of habitat (= study area) and season on survival and recruitment rates were evaluated by analysis of variance (Nie et al. 1975).

Seasonal survival rates of snowshoe hares did not differ significantly between habitats during the spring, summer, or winter periods of 1978 (summer: $F = 0.96$; 3,16 df; $P = 0.44$; fall: $F = 0.30$; 3,12 df; $P = 0.82$; winter: $F = 0.30$; 3,8 df; $P = 0.82$) (Figure 29) or 1979, although survival rates tended to differ among habitats during the summer 1979 (summer: $F = 2.37$; 3,24 df; $F = 0.10$; fall: $F = 0.73$; 3,12 df; $P = 0.36$; winter: $F = 1.81$; 3,8 df; $P = 0.22$). During the summer of 1979, survival rates of animals on the aspen grid tended to be lower than in other habitats. No significant changes in survival rates between seasons were apparent in 1978 ($F = 1.35$; 2,36 df; $0.50 > P$) or 1979 ($F = 0.74$; 2,44 df; $0.50 > P > 0.25$).

Recruitment rates within each season also did not differ significantly among the four habitats during 1978 (summer: $F = 0.47$; 3,16 df; $P = 0.71$; fall: $F = 0.14$; 3,12 df; $P = 0.94$; winter: $F = 0.31$; 3.8 df; $P = 0.82$) or 1979 (summer: $F = 0.59$; 3,24 df; $P = 0.63$; fall: $F = 1.25$; 3,12 df; $P = 0.34$; winter: $F = 2.23$; 3,8 df; $P = 0.16$) (Figure 30). Recruitment rates, however, did change significantly between seasons in both years (1978: $F = 9.96$; 2,36 df; $0.005 > P$; 1979: $F = 4.12$; 2,44 df; $0.05 > P > 0.01$). In both 1978 and 1979, recruitment rates were highest during the summer (the period of reproductive activity), declined during the fall, and increased slightly during the winter.

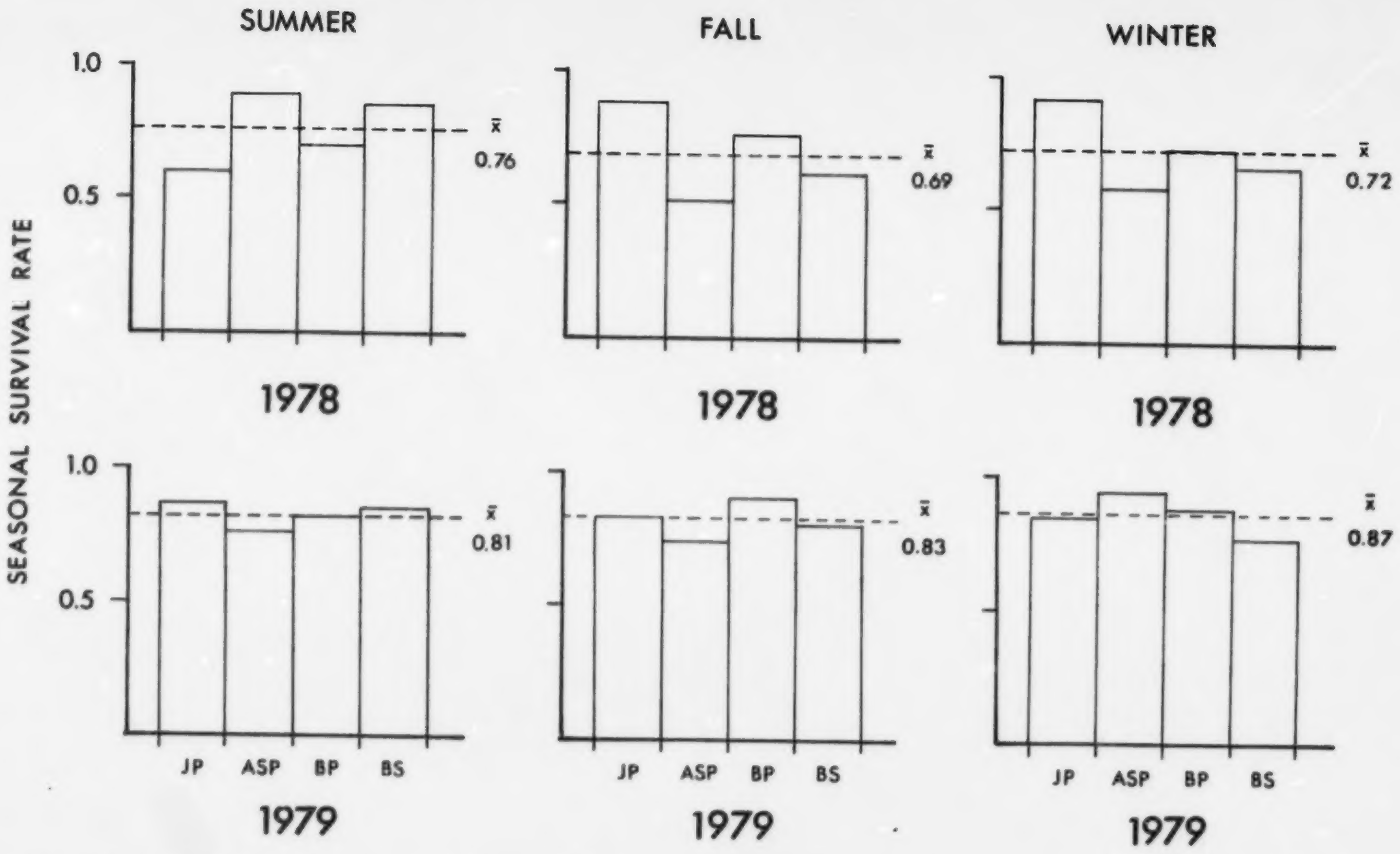

Figure 29. Seasonal survival rates of *L. americanus*. (Mean rates for each study area were obtained from MRA described in the text. Abbreviations for study areas are: JP = Jack Pine, ASP = Aspen, BP = Balsam Poplar, and BS = Black Spruce.)

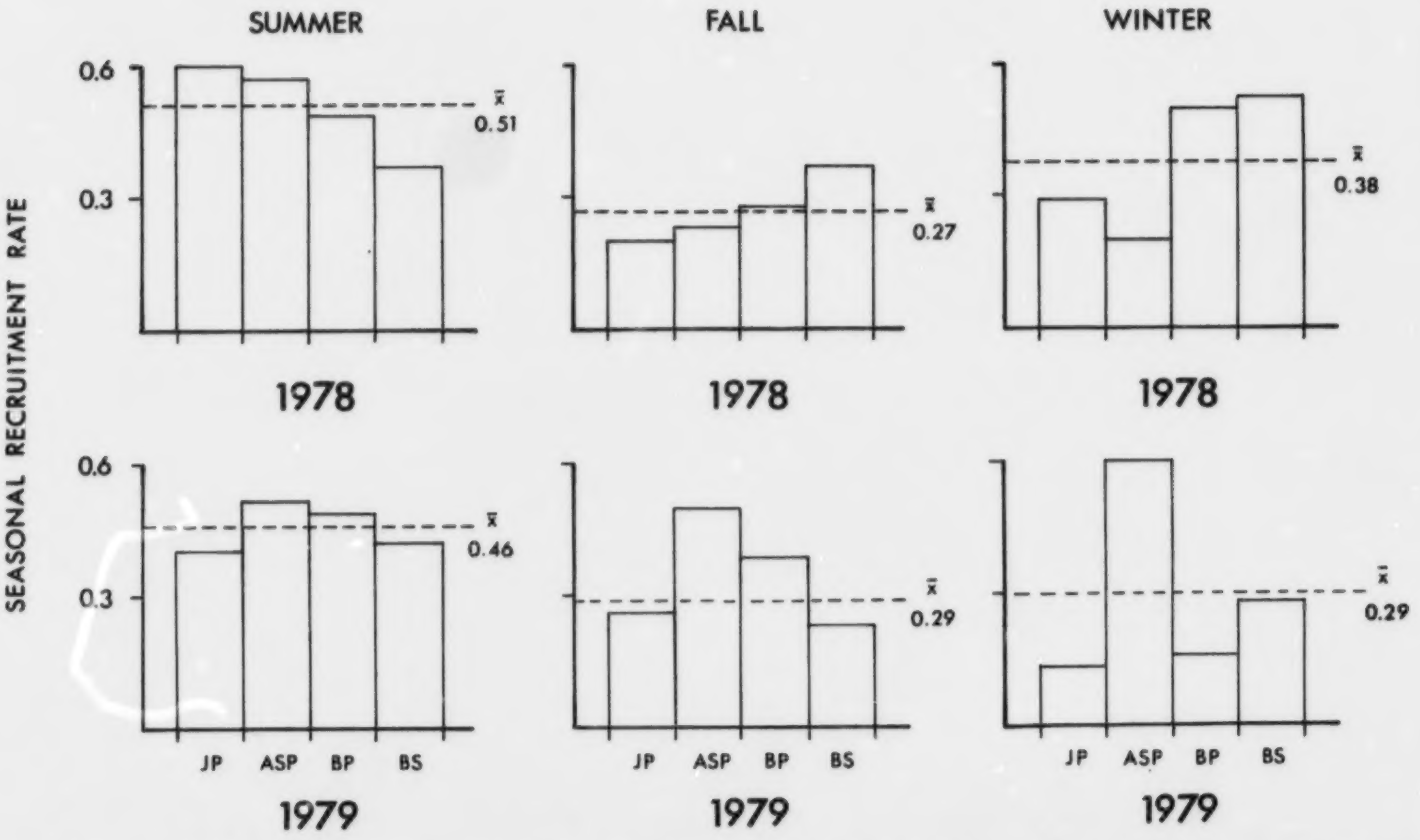

Figure 30. Seasonal recruitment rates of *L. americanus*. (Mean rates for each study area were obtained from MRA described in the text. Abbreviations for study areas are: JP = Jack Pine, ASP = Aspen, BP = Balsam Poplar, and BS = Black Spruce.)

6.2.4 Population Structure

6.2.4.1 Age distributions. Three age classes of snowshoe hares were recognized (juveniles, sub-adults, and adults) based on genital morphology (Trapp 1962) and previous trapping history. Adults were animals that had survived at least one winter. Sub-adults and juveniles were animals born that year.

In 1978, juveniles were most abundant at the start of the trapping season in July and declined gradually during August and September, reflecting the recruitment of juveniles to the sub-adult portion of the population (Figures 31 to 34). No or few juveniles were present in the overwintering populations. In 1979, juveniles increased rapidly in late May and June reaching peak numbers in August and September (with the exception of the population on the balsam poplar grid where juveniles reached peak numbers in July). No juveniles were present in any of the study populations by early November 1979.

Sub-adults generally increased over the summer (as juvenile cohorts matured), becoming most abundant in November. Few sub-adults were captured on the Jack Pine study area. During the winter of 1978-1979, most animals on the Aspen, Balsam Poplar, and Black Spruce study areas were sub-adults. In contrast, no sub-adults were present on the Jack Pine study area. During the early winter of 1979-1980, all study populations, except the jack pine population, were composed of approximately equal numbers of sub-adults and adults.

Only low to moderate numbers of adult snowshoe hares were present on the Aspen, Balsam Poplar, and Black Spruce study areas in 1978 and 1979 except during May and early June 1979 when almost all the animals present were adults. In contrast, adult animals were abundant on the Jack Pine study area throughout both years. All animals overwintering on the Jack Pine study area in 1978-79 were adults, whereas only a moderate number of adults overwintered on the other three study areas.

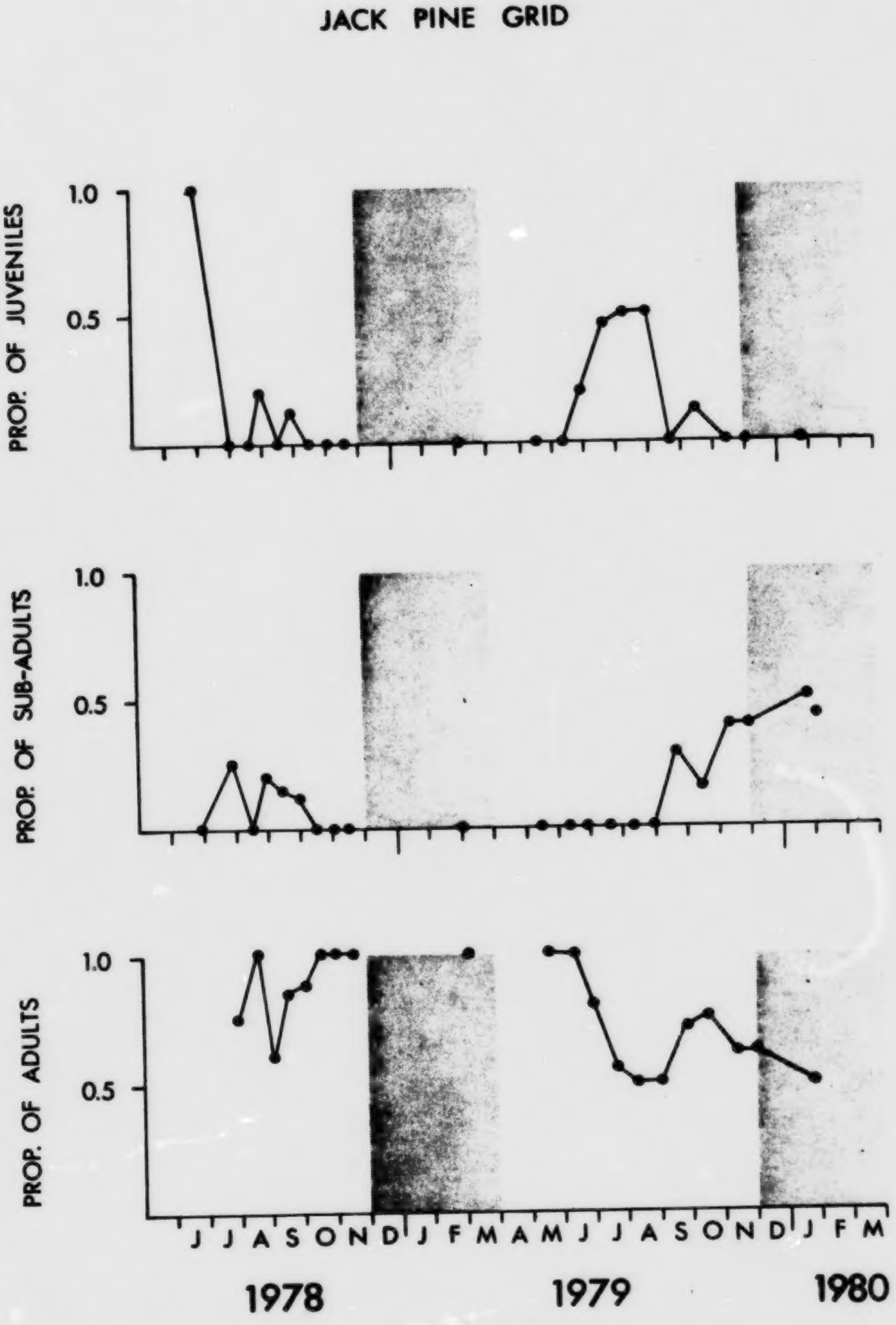

Figure 31. Age distributions of *L. americanus* on the Jack Pine study area. (Proportions are based on the actual number of animals captured in each trapping period; $0 \leq N \leq 13$. The winter periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

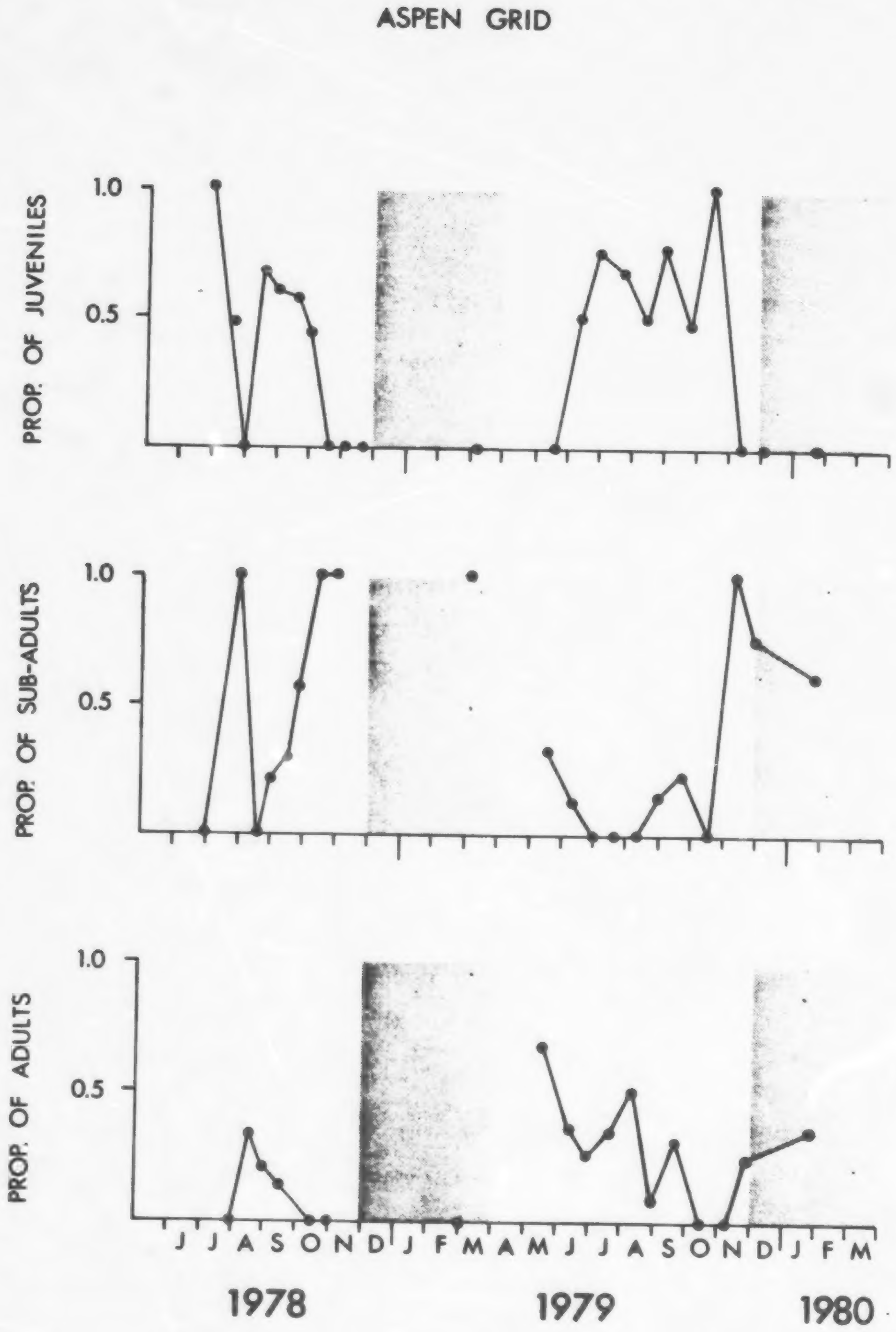

Figure 32. Age distributions of *L. americanus* on the Aspen study area. (Proportions are based on the actual number of animals captured in each trapping period; $0 < N < 13$. The winter trapping periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

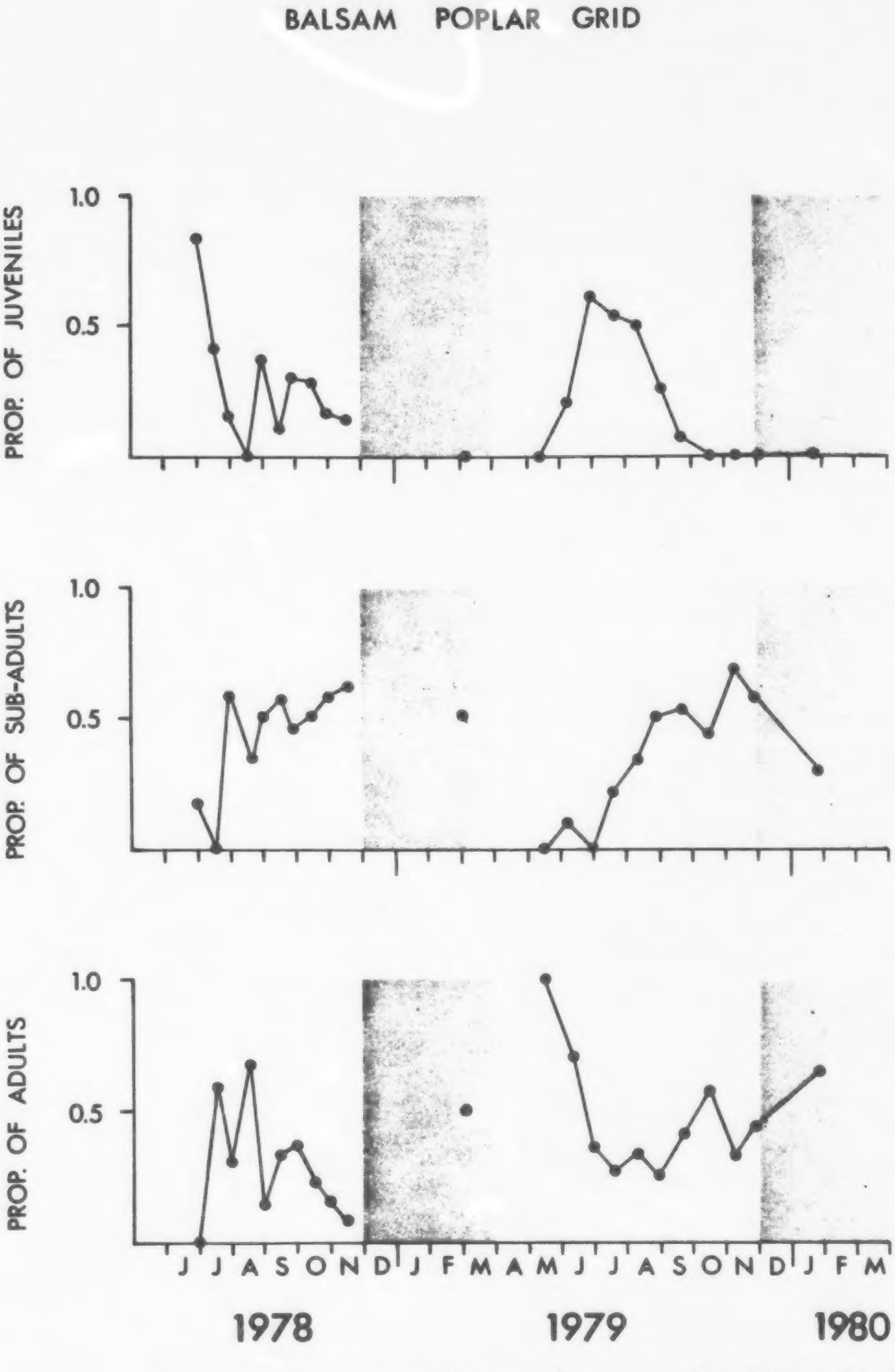

Figure 33. Age distributions of *L. americanus* on the Balsam Poplar study area. (Proportions are based on the actual number of animals captured in each trapping period; 5 ≤ N ≤ 28. The winter trapping periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

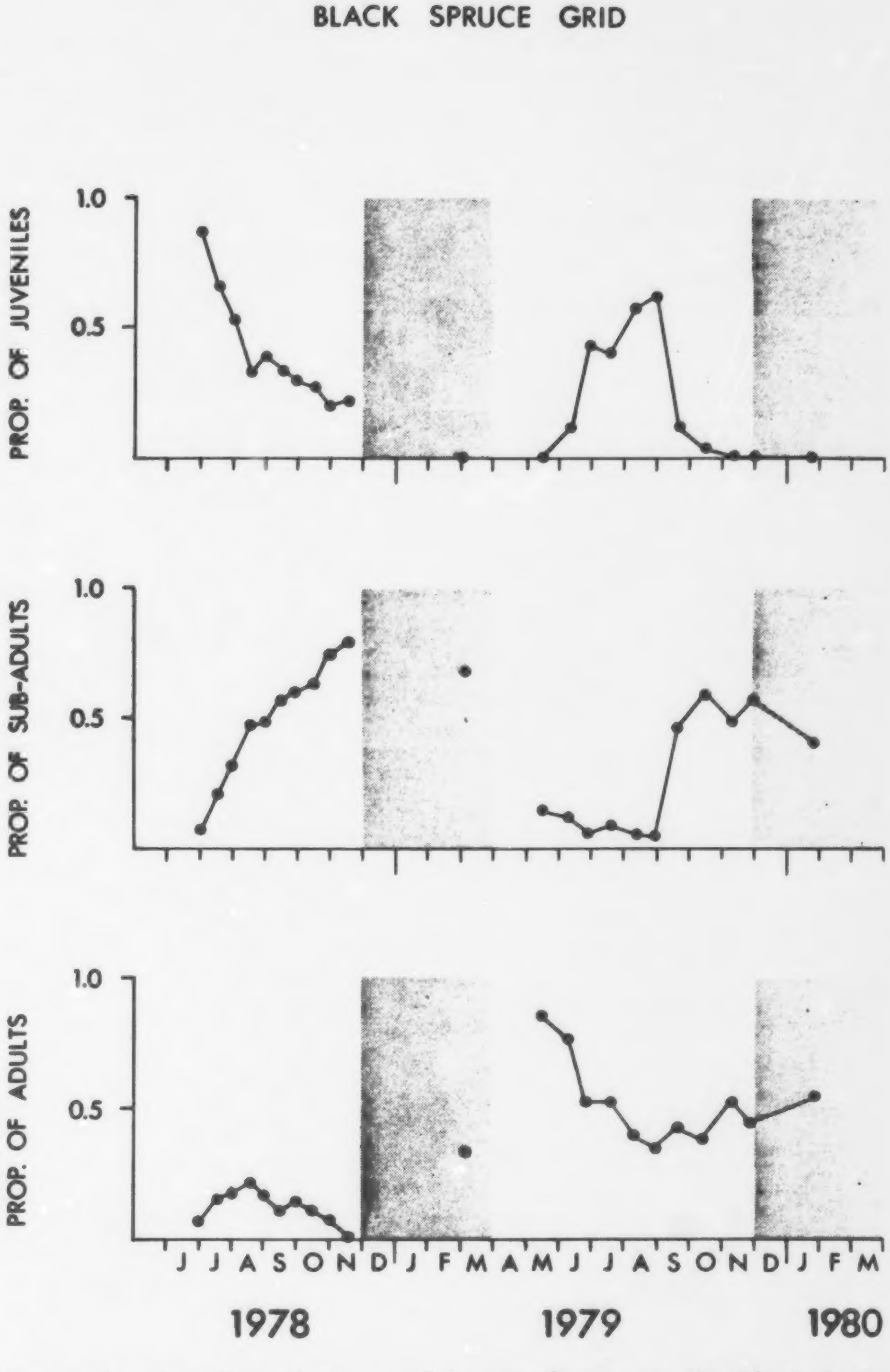

Figure 34. Age distributions of *L. americanus* on the Black Spruce study area. (Proportions are based on the actual number of animals captured in each trapping period; 13 ≤ N ≤ 32. The winter trapping periods, when trapping efforts were less intensive, are indicated by the shaded areas.)

6.2.4.2 Sex ratio. Sex ratios, expressed as the proportion of the total MNA that were males, were calculated for snowshoe hares on each study area during each trapping period (Figures 25 to 28). In all cases, sex ratios on each of the four study areas did not differ significantly[1] from 0.5.

6.2.5 Reproduction

As discussed earlier for small rodents, assuming that habitat selection is related to reproductive success, the mean number of young within each litter that survives to breeding age would be one of the better measures of habitat quality. However, because of the difficulty in obtaining such a measure in free-ranging populations of snowshoe hares, three indices of reproductive success were used in this study: breeding activity, pregnancy rates; and juvenile recruitment.

6.2.5.1 Breeding activity. Reproductive attributes of snowshoe hare populations on each of the study areas were assessed using external indices of reproduction. Male hares were considered to be in breeding condition only if their testes were obviously scrotal. Females were considered to be in breeding condition if their nipples were enlarged. Females were noted as being pregnant if the abdomen obviously was distended and/or if an obvious reduction in body weight was associated with an increase in the size of the nipples. Indices of breeding activity, expressed as the proportion of adult males and females that were in breeding condition during the summer period of 1978 (1 July to 20 September) and 1979 (16 May to 20 September) were determined for animals on each study area (Appendix 11.4, Table 65).

During the summer of 1978, breeding activity of male and female *L. americanus* did not differ significantly among habitats [Friedman's two-way ANOVA (Siegel 1956); males: $\chi^2 = 1.10$; $N_r = 6$; $k = 3$; $P = 0.78$; females: $\chi^2 = 0.60$; $N_r = 6$; $k = 3$; $P = 0.90$].

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[1] Yates correction for continuity employed.

In 1979, however, male breeding activity did differ among habitats ($\chi^2 = 11.7$; $N_r = 7$; $k = 3$; $P = 0.01$), whereas female breeding activity did not ($\chi^2 = 1.05$; $N_r = 7$; $k = 3$; $P = 0.79$). Fewer male *L. americanus* on the Aspen study area were in breeding condition during the summer of 1979 than in the other three habitats.

6.2.5.2 Pregnancy rates. Pregnancy rates, expressed as the proportion of adult female hares captured one or more times during the summer period of 1978 and 1979 that were pregnant, were calculated for each study population. In 1978, pregnancy rates were highest on the Black Spruce [0.38; N (total number mature females capture) = 8] and Jack Pine (0.33; N = 3) study areas followed by the Balsam Poplar (0.29; N = 7) and Aspen (0.00; N = 2) study areas. In 1979, pregnancy rates were again highest on the Black Spruce study area (0.52; N = 23) followed by the Balsam Poplar (0.46; N = 13), Jack Pine (0.30; N = 10), and Aspen (0.11; N = 9) study areas.

6.2.5.3 Juvenile recruitment. Juvenile recruitment rates, expressed as the number of new juvenile animals captured per adult female during each summer trapping period, were used as a third index of reproductive success. Juvenile recruitment rates, summarized in Appendix 11.4; Table 66, were compared among study areas using Friedman's two-way ANOVA.

During the summer 1978, juvenile recruitment rates tended to differ among habitats ($\chi^2 = 6.55$; $N_r = 6$; $k = 4$; $0.10 > P > 0.05$); recruitment of juveniles tended to be highest on the Black Spruce study area and was lowest on the Jack Pine study area. No significant differences in juvenile recruitment rates were apparent in 1979 ($\chi^2 = 4.26$, $N_r = 7$; $k = 4$; $0.30 > P > 0.20$).

6.2.6 Condition

Studies by Keith (1963) and Dolbeer and Clark (1975) have suggested that habitat preferences and use by *L. americanus* may partially reflect the quality and quantity of browse locally available. Variation in browse may in turn affect the condition of snowshoe hares. Body weights were used in this study as an index of condition of juveniles, sub-adults, and adults on each study area and are summarized in Appendix 11.4, Table 67.

Body weights of juvenile snowshoe hares differed significantly among study areas only in 1978 (Friedman's two-way analysis of variance; 1978: $\chi^2 = 9.3$; $N_r = 9$; $k = 3$; $0.05 > P > 0.01$; 1979: $\chi^2 = 2.9$; $N_r = 7$; $k = 4$; $0.50 > P > 0.25$). Juvenile snowshoe hares on the Jack Pine study area in 1978 were significantly smaller than juveniles on the Balsam Poplar study area [two-way multiple comparison test (Hollander and Wolfe 1973); $P < 0.05$]

Body weights of sub-adult snowshoe hares tended to differ among the four study areas in 1978 ($\chi^2 = 7.4$; $N_r = 8$; $k = 4$; $0.10 > P > 0.05$) and differed significantly among these habitats in 1979 ($\chi^2 = 20.8$; $N_r = 11$; $k = 4$; $P < 0.00$). In 1978, sub-adults on the Aspen study area tended to be smaller than sub-adults on the Jack Pine study area ($P < 0.10$), whereas sub-adult hares on the Jack Pine study area in 1979 were significantly smaller than sub-adults on the remaining three study areas ($P < 0.05$).

Body weights of adult snowshoe hares differed significantly among study areas in both years (1978: $\chi^2 = 9.1$; $N_r = 9$; $k = 4$; $0.05 > P > 0.01$; 1979: $\chi^2 = 17.3$; $N_r = 11$; $k = 4$; $P < 0.00$). Adult hares on the Jack Pine study area in 1978 were smaller than those on the Aspen study area ($P < 0.05$). In 1979, adults on the Black Spruce study area were significantly smaller than adult hares on the Aspen study area ($P < 0.001$) and tended to be smaller than those on the Balsam Poplar study area ($P < 0.10$).

6.3 HABITAT USE

The response of *L. americanus* to major habitat types and vegetation structure of the boreal forest ecotone was assessed by two methods: comparisons of the peak population sizes on each study

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[1] Mean body weights for cells with no captures were estimated by interpolation.

area; and multivariate analyses of snowshoe hare abundance and habitat structure.

6.3.1 Peak Population Sizes

Habitat use by snowshoe hares commonly has been assessed by comparisons of indices of abundance such as the number of captures, the number of tracks/unit distance, or population densities in different habitat types (e.g., Keith and Surrendi 1971; Dolbeer and Clark 1975; Keith and Windberg 1978). In this study, peak MNA estimates were used as an index of habitat use during each year of the study.

Peak population sizes on the Jack Pine, Aspen, Balsam Poplar, and Black Spruce study areas during the period of 1 July to 9 November 1978 were 11, 15, 21, and 46 snowshoe hares, respectively. In 1979, black spruce forest was again the most commonly used habitat (peak MNA = 38) followed by balsam poplar (28), jack pine (16)[1], and aspen forest (15)[1].

Based on MNA estimates for early March 1978, snowshoe hares most frequently used black spruce and balsam poplar habitats (24 and 22, respectively) during the mid-winter, whereas few animals were present in jack pine and aspen cover types (six and seven, respectively). In late January 1980, snowshoe hares again were most abundant in black spruce forest (19); lower numbers were present in balsam poplar (13), aspen (10), and jack pine (9) habitats.

6.3.2 Multivariate Analyses of Snowshoe Hare--Habitat Relationships

Indices of abundance within major habitat types can provide crude estimates of habitat factors affecting local distributions of snowshoe hares but may ignore other factors which may be important in the categorization of major habitat types. As discussed earlier for small rodents, multivariate statistical techniques permit simultaneous consideration of all habitat data and so avoid the necessity for arbitrary classifications of habitat type.

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[1] Trappability was less than 50%; MNA shown are likely underestimates.

The relationship between the local distribution (and abundance) of *L. americanus* and vegetation structure were assessed by a two-stage multivariate analysis. Initially a BMDP4M factor analysis (Dixon and Brown 1979) was used to reduce a possible set of 28 habitat variables to nine independent factors that characterized vegetation structure on the four live-trapping areas (see Appendix 11.4 for details). Interpretations of the nine independent factors based on orthogonally-rotated factor loadings (Appendix 11.4, Table 68) greater than ± 0.250 are summarized in Table 25. The relationship between these factors and the local distribution and abundance of snowshoe hares were then assessed using stepwise multiple regression (SMR) analyses. Separate SMR's were run for snowshoe hare populations during the summer period of 1978 and 1979, and for the mid-winter period of 1978-1979 and 1979-1980, using the BMDP2R analysis (Dixon and Brown 1979).

The number of captures per trap-night (CTN) was used as an index of snowshoe hare abundance. One estimate of CTN was calculated for each trapping station on each study area for the periods of 1 July to 27 October 1978 and 16 May to 13 October 1979. Estimates of CTN for the mid-winter of 1978-1979 included all animals captured between 27 October 1978 and 3 March 1979; mid-winter estimates in 1979-1980 included all captures between 9 November 1979 and 25 January 1980. For each period, CTN were determined by dividing the cumulative number of captures of snowshoe hares by the cumulative number of trap-nights corrected for the number of trap setoffs (e.g., accidental trips, captures of other species). All estimates of CTN were transformed by taking the log of (CTN + 1) to correct for heteroscedasticity and non-normality (Sokal and Rohlf 1969).

6.3.2.1 Summer 1978. During the summer of 1978, 33.6% of the variance in the abundance of *L. americanus* could be explained by habitat structure (Appendix 11.4; Table 69). All five predictor variables (+aspen/-black spruce forest, +white spruce/-black spruce

Table 25. Description of habitat variables that characterize the nine factors of the snowshoe hare study area factor analysis. (Rotated factor loadings are shown in Appendix 11.4, Table 68. Only variables whose factor loadings were greater than ±0.250 are included in the descriptions. Names assigned to each factor are used in all further discussions of this analysis.)

Factor	Name	Description of Variables
1	Balsam poplar forest	- characterized by a predominance of *Alnus* spp., *C. stolonifera*, and *Viburnum* spp. shrub cover; a moderate to dense forest canopy dominated by *P. balsamifera*; and moderate to dense ground cover dominated by *Equisetum* spp.
2	+Aspen/-Black spruce forest	- measures the presence of a number of variables describing aspen forest habitat and the absence of variables describing black spruce-tamarack forest types. Aspen variables included the presence of a tree canopy dominated by *P. tremuloides*; shrub layer characterized by *A. alnifolia*, *S. canadensis*, and *Rosa* spp.; and high densities of *A. uva-ursi* and *V. myrtilloides*. Variables associated with black spruce habitat included a forest canopy composed largely of *P. mariana* and moderate densities of *L. laricina*; moderate densities of *Salix* spp. and ground cover characterized by a dense growth of moss and *L. groenlandicum*; and moderately dense *V. vitis-idaea*.
3	+White spruce/ -Black spruce forest	- represented by the presence of variables associated with white spruce forest cover and the absence of variables associated with black spruce-tamarack habitats. White spruce variables included a forest canopy composed largely of *P. glauca*; a shrub layer of *S. canadensis* and *Rosa* spp.; and a high density of *C. canadensis*. Black spruce-tamarack variables included a forest canopy dominated by *P. mariana* and *L. laricina*, and a shrub layer commonly composed of *Salix* spp.
4	Open Habitat	- characterized by a sparse tree and ground cover (i.e., trees and ground cover rarely present) and a limited growth of shrubs.
5	Jack pine understory	- measures the presence of variables typical of jack pine forest such as a paucity of shrub cover and dense growths of *Cladina/Cladonia* spp.; and the absence of variables commonly associated with more poorly-drained sites such as *L. laricina*, *Salix* spp., and a high density of moss cover.
6	Shrub birch-white spruce transition	- characterized by a predominance of *B. glandulosa*, sparse to moderate densities of *P. glauca*, moderate densities of *L. groenlandicum* and an absence of *V. vitis-idaea*.
7	*V. caespitosum*	- reflects a dense growth of *V. caespitosum*, low to moderate densities of *Cladina/Cladonia* spp. and an absence of *V. uliginosum* and *S. canadensis*.
8	Bluebell Cover	- is a measure of vegetation associated with dense growths of *M. paniculata*; low densities of *Alnus* spp., *P. balsamifera*, *Rosa* spp., and *L. laricina*; and an absence of moss cover.
9	Paper Birch	- measures a tree canopy composed almost entirely of *B. papyrifera* and moderate to low densities of *Viburnum* spp.

forest, jack pine understory, shrub birch-white spruce transition, and balsam poplar forest cover) were negatively correlated with the abundance of snowshoe hares.

Of the five habitat factors, the +aspen/-black spruce factor was most strongly associated with snowshoe hare abundance (accounting for 16.6% of the variance). After this was taken into account, the +white spruce/-black spruce factor explained an additional 8.0% of the variance in abundance. The remaining three habitat factors were statistically significant predictors of abundance but each accounted for only 1.9 to 4.8% of the total variance.

How then do these relationships between habitat structure and abundance of snowshoe hares relate to major habitat types of the boreal forest? Expected numbers of CTN were calculated for each study area using the SMR equation (Appendix 11.4, Table 69) and the mean factor scores for each habitat (Appendix 11.4, Table 70). During summer 1978, black spruce forest was associated with the highest index of abundance (Table 26). In contrast, jack pine habitat was associated with the lowest numbers of snowshoe hares. Results suggest that of the four habitats studied, black spruce forest was most suitable for *L. americanus*.

6.3.2.2 Summer 1979. During the summer of 1979, three habitat factors accounted for 28.1% of the variance in the number of captures of snowshoe hares. Jack pine understory, +white spruce/-black spruce forest, and +aspen/-black spruce forest all were negatively correlated with the abundance of snowshoe hares (Appendix 11.4, Table 71). Of the three significant predictor variables, the +aspen/-black spruce factor accounted for most (20.3%) of the variance in numbers of snowshoe hares. The +white spruce/-black spruce forest factor and the jack pine understory factor were both significant predictors of abundance but only explained an additional 4.9 and 2.9% of the total variance, respectively.

Based on the SMR model and the mean factor scores for each predictor variable on each study area, higher numbers of snowshoe hares were most often associated with black spruce forest cover

Table 26. Expected number of CTN during the summer and winter of 1978 and 1979. (Expected number of CTN for one trap station in each habitat was calculated using the appropriate SMR equation for that season and the mean factor scores for each habitat.)

Season	Study Area			
	Jack pine	Aspen	Balsam poplar	Black spruce
Summer 1978	0.0169	0.0211	0.0245	0.0493
Winter 1978-1979	0.0077	0.0113	0.0086	0.0283
Summer 1979	0.0280	0.0170	0.0432	0.0640
Winter 1979-1980	0.0002	0.0010	0.0012	0.0022

(Table 26). Conversely, aspen and jack pine forests commonly were associated with lower numbers of this species.

6.3.2.3 Winter 1978-1979. Only 14.9% of the variance in the abundance of snowshoe hares during the winter of 1978-1979 was explained by habitat structure (Appendix 11.4, Table 72). Habitat factors associated with +aspen/-black spruce forest cover were negatively correlated with snowshoe hare numbers and explained 6.0% of the variance in abundance. Similarly, habitat factors associated with jack pine understory, balsam poplar forest, +white spruce/-black spruce forest, and shrub birch-white spruce transition were negatively associated with abundance but explained only 1.3 to 2.7% of the remaining variance in numbers.

Expected numbers of captures, as predicted by the SMR model and mean factor scores, indicated that aspen and black spruce forests were most commonly associated with higher numbers of snowshoe hares during the winter of 1978-1979 (Table 26). Jack pine and balsam poplar habitats, on the other hand, were associated most often with lower numbers of *L. americanus*.

6.3.2.4 Winter 1979-1980. During the winter of 1979-1980, habitat structure explained only 10.1% of the variation in snowshoe hare numbers (Appendix 11.4, Table 73). As during the previous winter, the +aspen/-black spruce forest and jack pine understory factors were most strongly associated with snowshoe hare abundance. However, both the +aspen/-black spruce forest and the jack pine understory factors were negatively associated with snowshoe hare abundance.

Based on expected numbers of captures, black spruce forest was associated most commonly with higher numbers of snowshoe hares during the winter of 1979-1980 (Table 26). In contrast, jack pine habitats were associated with low numbers during the same period.

6.3.2.5 Inter-season comparisons of SMR models. SMR analyses for the spring to summer period of 1978 and 1979 accounted for approximately the same amount of variation in the abundance of snowshoe hares (33.6% vs 28.1%). The three major predictor variables in both SMR models were identical and accounted for similar proportions of the total explained variance in both years. In addition, all were negatively correlated with snowshoe hare abundance. This suggests that snowshoe hares were responding to similar components of vegetation structure during the spring to summer period of each year.

The SMR models for winter abundance of snowshoe hares accounted for less of the variance in captures than the spring-summer models but included almost identical predictor variables. The similarity of the spring-summer and winter models suggests that seasonal factors had only a minor effect on the habitat affinities of snowshoe hares and that similar components in habitat structure influenced local distributions of this species throughout the entire year.

6.4 DISCUSSION

6.4.1 Population Trends

Keith and Windberg (1978) used a mid-winter questionnaire of registered trappers to monitor long-term population trends of snowshoe hares in Alberta. Based on information for the Athabasca Basin during the period from 1963 to 1976 [Keith and Windberg (1978), Figure 4, Area D], the last population peak occurred in the mid-winter of 1971. Assuming that population cycles in snowshoe hares occur every 8 to 11 years (Keith 1963), the next population peak in this region should occur during the period of 1979 to 1982. It is probable then that the four study populations enumerated during this research program were either in the increase phase or peak phase of their population cycle.

Snowshoe hares were more abundant on the Jack Pine and Balsam Poplar study areas in 1979 than in 1978, suggesting that snowshoe hare populations were still increasing in the Athabasca region. Assuming that population estimates on the Aspen study area in 1979 were underestimates (as suggested by the poor trappability of animals on this area), this population also may have increased between 1978 and 1979. In contrast, the population on the Black Spruce study area appeared to have changed little between years.

6.4.2 Population Characteristics and Habitat Quality

As discussed earlier in relation to small rodents (Section 4.4), habitat selection and use by different species of small mammals are the expression of a complex response of an animal to a large number of independent and interdependent variables that reflect the increased reproductive success of animals able to select optimal habitat types (Krebs 1978). The characteristics of a population, particularly those related to reproductive success, consequently should reflect the 'quality' of its habitat. The apparent density-dependent dispersal of snowshoe hares (particularly young animals) from areas of high quality habitat to more marginal habitats (Keith 1963; Dolbeer and Clark 1975) similarly suggests that variations in population characteristics are associated closely with habitat quality. Assuming that habitat selection is related to reproductive success, populations in higher quality habitats should be characterized by moderate to high numbers of animals, high survival, high recruitment of juvenile animals, high reproductive activity, balanced sex ratios and age structures, and average to good nutritional condition.

However, because some demographic parameters of snowshoe hares vary with cyclic fluctuations in density, indices of habitat quality based on population characteristics must be used with caution. For example, Keith and Windberg (1978) showed that overwinter juvenile survival, adult survival, growth (and weight losses), the length of the breeding season, ovulation rates, and pregnancy rates of snowshoe hares were associated with cyclic changes in population densities. Assuming that these demographic changes are similar among synchronously fluctuating populations of snowshoe hares, comparisons of characteristics of synchronous populations should minimize the probability of attributing cyclic demographic changes with differences between habitats. Although it is not possible on the basis of 2 years of study to determine if the four study populations discussed here were synchronous, previous work by Keith and associates (Keith 1963; Keith and Windberg 1978) suggest that cyclic population changes are regionally synchronous. Characteristics consequently have been compared between all four study populations with the provision that some differences among populations may reflect cyclic rather than inter-habitat differences in demography.

6.4.2.1 Population size and structure. Differences in peak MNAs suggest that the carrying capacity of jack pine, aspen, balsam poplar, and black spruce forests differed (Table 27). Population trends in each habitat, however, suggest that these four communities were stable habitats for snowshoe hares [i.e., snowshoe hares were able to inhabit the communities throughout the year (Douglass 1976a)].

Age structures, however, were partially influenced by differences in habitat (Table 27). In particular, few young animals were captured on the Jack Pine study area implying that reproductive success was limited. In contrast, recruitment of young animals on the Black Spruce study area was high and appeared to be associated with the rapid increase in numbers. These differences in age structures imply that jack pine forest was marginally suitable, whereas aspen and balsam poplar forests were moderately suitable and black spruce forests were optimal habitats for snowshoe hares.

6.4.2.2 Reproductive success and habitat quality. Overall patterns of breeding activity observed in this study appeared to be similar to those observed in a number of other studies of snowshoe hares (Rowan and Keith 1956; Adams 1959; Newson 1964; Bookhout 1965; Dodds 1965;

Table 27. Characteristics of *L. americanus* populations on the four study areas (July 1978 to January 1980).

Characteristic	Jack pine	Aspen	Balsam poplar	Black spruce
Population trends	- small increase in numbers between 1978 and 1979; moderate seasonal increase to Sept., decline in late fall and over winter	- similar population size in both years; moderate seasonal increase to Sept., decline in late fall and over winter	- moderate increase in numbers between 1978 and 1979; moderate seasonal increase to Oct. and Nov.; little change in population size over winter	- moderate decline between 1978 and 1979; rapid increase in July to Aug. 1978; decline in fall and over winter; moderate increase to Aug. in 1979
Peak MNA: 1978	11	15	21	46
1979	15	16	28	38
Age Structure: Summer/Fall[a]	- mostly A; J increase in June to Aug. (1979); SA most common in fall	- large proportions of J May to Oct.; moderate to low proportions of A in early summer, decline to low numbers by fall; SA increase in fall	- J abundant until late July; moderate to low proportions of A throughout summer and fall; increase in SA in fall	- J abundant during July to Aug.; few A in 1979, moderate numbers in 1979; increase in SA in fall
Winter (1978-79)	- all adults	- all sub-adults	- sub-adults and adults	- mostly sub-adults, some adults
Sex Ratio[b]	- equal	- tendency towards more females in 1978 and more males in 1979	- equal	- equal
Breeding activity				
Males	- average	- average 1978; below average 1979	- average	- average
Females	- average	- average	- average	- average
Pregnancy Rates	- moderate	- low	- moderate to high	- highest
Juvenile Recruitment	- low 1978; average 1979	- moderate 1978; average 1979	- moderate 1978; average 1979	- high 1978; average 1979
Body Weights:				
Juveniles	- smaller 1978; average 1979	- average	- average	- average
Sub-adults	- average 1978; smaller 1979	- smaller	- average	- average
Adults	- smaller 1978; average 1979	- average	- average	- smaller
Survival: Summer	- below average 1978; average 1979	- slightly above average 1978; average 1979	- average	- slightly above average 1978; average 1979
Fall	- above average 1978; average 1979	- below average	- slightly above average	- average
Winter	- above average 1978; average 1979	- below average 1978; average 1979	- average	- slightly below average

continued...

Table 27. Concluded.

Characteristic		Jack pine	Aspen	Balsam poplar	Black spruce
Recruitment:	Summer	- above average 1978; average 1979	- above average	- average	- below average 1978; average 1979
	Fall	- below average	- below average 1978; above average 1979	- average 1978; below average 1979	- above average 1978; average 1979
	Winter	- below average	- below average 1978; above average 1979	- above average 1978; below average 1979	- above average 1978; average 1979
Dispersal Index[d]:					
Summer		- high 1978; limited 1979	- high in situ recruitment 1978 moderate 1979	- limited	- limited
Fall		- limited 1978; moderate 1979	- high mortality 1978; high 1979	- limited	- moderate 1978; limited 1979
Winter		- limited; moderate mortality 1979	- high mortality 1978; limited 1979	- moderate 1978; low, some mortality 1979	- high 1978; moderate 1979

[a] J = juvenile, SA = sub-adult, A = adult.

[b] trends are indicated; no sex ratios were significantly different from 0.5.

[c] Dates shown are last period when 50% or more of the adult animals present were in breeding condition.

[d] Based on Fairbairn (1977a).

Keith et al. 1966; Wood and Munroe 1977; Keith and Windberg 1978); throughout much of their range, male and female snowshoe hares typically become reproductively active in February and March, respectively, and remain in breeding condition until August. Females commonly produce an average of three litters; first litters are usually born in early May to June, whereas the last are usually born in late August. In this study, the initiation dates of breeding and parturition are not known because populations were not sampled regularly during the late winter and early spring; however, the cessation of breeding and parturition observed was similar to that of previous studies.

Within the Athabasca Basin, however, some differences in reproductive success were apparent among habitats (Table 27). Pregnancy rates and juvenile recruitment were highest on the Black Spruce study area, whereas male breeding activity and pregnancy rates were low on the Aspen study area. This suggests that black spruce forest was optimal habitat for *L. americanus* in the Athabasca area. Aspen habitat, on the other hand, was a poor quality habitat for this species. Poor juvenile recruitment on the Jack Pine study area, despite average breeding activity and moderate pregnancy rates, suggests that this habitat is also a poorer quality habitat for snowshoe hares.

6.4.2.3 Nutritional condition and habitat quality. A number of studies have indicated that the nutritional condition of *L. americanus* and other leporids can affect reproduction and survival; assuming that differences in habitat structure can influence nutrition of snowshoe hares, indices of nutritional condition should provide an additional index of habitat quality. For example, Hill (1972) showed that litter sizes of *Sylvilagus floridanus* (cottontail rabbits) in Alabama were correlated with soil pH and suggested that soil fertility, through its influences on plant types and quality, influenced litter sizes of cottontail rabbits. Kirkpatrick and Keebe (1971) similarly showed that low nutritional diets reduced reproductive activity. Following a forest fire in central Alberta, Keith and Surrendi (1971) associated the low pregnancy rates of snowshoe hares in burned areas, in relation to those of animals in unburned communities, with the sharp decline in habitat quality in severely burned areas.

The nutritional condition of snowshoe hares also appears to affect survival rates. Using body weight as an indicator of condition and body size, Keith and Windberg (1978) found that survival rates of adult and juvenile animals during the winter tended to be correlated directly with the condition of the animals. Similarly, Pease et al. (1979) showed that malnourished snowshoe hares survived poorly during winters with colder temperatures.

Assuming that body weight is an adequate measure of condition, conditions of snowshoe hares in this study did appear to differ among habitats. In particular, snowshoe hares in jack pine forest communities were often in poorer condition (i.e., smaller body weights) than animals in the remaining habitats. Other differences in condition among the four study areas were not consistent among age classes on the same area or between years, suggesting that the conditions of animals on the Aspen, Balsam Poplar, and Black Spruce study areas were similar. Differences in condition consequently imply that jack pine forest was a marginal habitat for snowshoe hares, whereas aspen, balsam poplar, and black spruce forests were more suitable habitats for this species.

6.4.2.4 Dispersal and habitat quality. Survival and recruitment are both important aspects of population change; populations in higher quality habitats should be characterized by low mortality rates and high natality, whereas populations in marginal habitats should be characterized by higher mortality rates and low natality. Further, if surplus snowshoe hares are forced out of more heavily populated areas of preferred or higher quality habitat into areas of marginal habitat as suggested by Keith and Surrendi (1971) and Dolbeer and Clark (1975), populations in marginal habitats also should be characterized by high immigration. Conversely, populations in higher quality habitats should be characterized by higher rates of emigration, particularly during periods of population increases. To assess the relative importance of mortality and emigration in population losses and of natality and immigration in population increases, seasonal survival and recruitment rates were compared within each season, as described previously for small rodents (Section 3.6.2.1).

During the summer of 1978, dispersal on the Jack Pine study area was high, suggesting that most animals recruiting to this population were immigrants (Table 27). In contrast, dispersal was limited during the summer of 1979 implying that increases in the population during this period were largely the result of young born on the area. Dispersal was low during the fall of both years and remained low during the winter--the overwinter decline in numbers (Figure 25) thus would appear to be due to mortality rather than immigration.

Dispersal of snowshoe hares on the Aspen study area was low throughout 1978 but increased during the summer and fall of 1979. Population increases in 1978 consequently would appear to be the result of juvenile recruitment, whereas increases in 1979 were principally due to immigration (Figure 26). Low survival and recruitment rates of snowshoe hares during the fall and winter of 1978 and during the winter of 1979 suggest that overwinter losses from this population were largely caused by increased mortality.

Throughout the summer of 1978 and 1979, dispersal indices of snowshoe hares in the Balsam Poplar study area were low (Table 27). Population increases during the summer, consequently are likely due to increased natality (Figure 27); this is supported by the increased numbers of juvenile and sub-adult animals recruiting to the population at this time (Figure 33). During the fall, however, dispersal remained low suggesting that losses of animals during this period were due to mortality and not emigration. Immigration (i.e., moderate dispersal) appeared to be the principal cause of a slight population increase during the winter of 1978-1979, whereas increased mortality resulted in a slight decline in numbers during the winter of 1979-1980.

Increases in population size on the Black Spruce study area in 1978 (Figure 28) appeared to be due mostly to the recruitment of sub-adults already on the area; dispersal indices were low throughout the summer and the proportions of sub-adults in the population increased rapidly during July and August (Figure 34). Dispersal also was limited during the summer of 1979, when both the number of animals and the proportion of juveniles in the population were increasing rapidly; most of this increase would appear, as a result, to be due to the recruitment of juveniles born on the study area. Dispersal indices increased in the fall and winter of both 1978 and 1979, coincident with a decline in numbers, thus implying that most losses during these periods were due largely to emigration.

How then do these indices of mortality, natality, and dispersal relate to habitat quality? Based on criteria discussed earlier, black spruce forest was the most suitable habitat for snowshoe hares; recruitment of young animals born on the area was high during both summers and population losses from peak populations in each year were attributed largely to emigration. Conversely, both aspen and jack pine forests were marginal habitats for snowshoe hares; fall declines in numbers were associated with increased mortality, whereas the small increase in numbers during the summer were due largely to immigration from surrounding areas. Increased recruitment of juveniles on the Jack Pine study area during the summer of 1979, however, suggests that habitat conditions on this area may have improved between 1978 and 1979. Balsam poplar communities were moderately suitable habitats for snowshoe hares; increases during both summers were associated with the recruitment of young born on the area, whereas declines during the fall and winter were attributable to both emigration and mortality.

6.4.2.5 Summary. Although snowshoe hares were able to inhabit jack pine, aspen, balsam poplar, and black spruce forest throughout the year, population characteristics suggest that the quality of these communities as snowshoe hare habitats did differ. Black spruce forests were the most suitable habitats; age structures were balanced, reproductive success was high, nutritional condition was average, juvenile recruitment during the summer was high, and most population losses were due to emigration. Balsam poplar communities were moderately suitable for snowshoe hares; age structures were balanced, reproductive success was moderate, in situ recruitment was moderate, and mortality during the fall and winter was moderate to low. In contrast, both aspen and jack pine forests were marginal habitats for snowshoe hares; few juveniles were present in jack pine forest, reproductive success in both habitats was low, animals in jack pine communities were in poor condition, population increases in both communities were largely the result of immigration, and declines were attributable mostly to increased mortality.

6.4.3 Habitat Use

Throughout their range in the boreal forest of North America, snowshoe hares appear to inhabit most commonly black spruce forest, spruce-fir forests, mixed spruce-fir-lodgepole pine forests, and post-fire successional areas dominated by aspen regrowth (MacLulich 1937; Bider 1961; Trapp 1962; Keith 1972; Dolbeer and Clark 1975; Wood and Munroe 1977; Keith and Windberg 1978). In this study, indices of habitat use, based upon peak population sizes during each year of trapping and on multivariate analyses of vegetation structure and snowshoe hare abundance, are in agreement with these studies; black spruce forest consistently supported the largest number of snowshoe hares, followed by balsam poplar, aspen, or jack pine forest. Indices of habitat quality based on population characteristics also ranked black spruce forests as an optimal habitat.

Keith (1972), however, concluded that optimal cover for snowshoe hares in northern Alberta was in areas of aspen regrowth following fires; the hazel, willow, and alder understory associated with this habitat apparently provided good cover and good winter food supplies for snowshoe hares. Mature conifer forests or mixed wood areas generally supported only low densities of snowshoe hares. Resident populations in these areas occurred chiefly in shrub-dominated areas or young coniferous cover along bog edges, water courses, or natural openings. The discrepancy in indices of use of aspen forests in this and Keith's (1972) study likely reflects differences in the successional age of these aspen habitats; the Aspen study area in this study was a mature stand of aspens, whereas Keith's (1972) study areas were located largely in early (post-fire) successional communities. As Keith (1972) discusses, older mature stands of aspen may be marginal habitats for snowshoe hares, whereas others still may provide high quality habitat; the period of time that aspen stands remain attractive to hares appeared related to both the density and composition of the shrub understory.

Multivariate analyses of snowshoe hare abundance and habitat structure indicated that some specific components of vegetation were associated with local distributions of snowshoe hares. Based on the summer and winter analyses, higher numbers of snowshoe hares were associated commonly with *L. laricina* and *P. mariana* tree cover and *Salix* spp. shrub cover. Ground cover types dominated by moss, *L. groenlandicum*, and *V. vitis-idaea* also were common components of several of the significant predictor variables of high snowshoe hare abundance. In contrast, no single habitat variable was associated consistently with low numbers of snowshoe hares, although *P. glauca* tree cover; *Rosa* spp. and *S. canadensis* shrub cover; and *V. uliginosum* and *Cladonia/Cladina* ground cover were components of at least two of the predictor variables that were associated most commonly with lower numbers of snowshoe hares. It should be stressed, however, that the associations between these habitat factors and snowshoe hare abundance do not necessarily imply a cause and effect relationship; snowshoe hares may be responding to other habitat variables (not measured in this study) which are also negatively or positively associated with these habitat components.

Habitat selection by snowshoe hares also appears to be partly influenced by changes in population densities. Keith (1963) and Keith and Windberg (1978) considered changes in habitat use by snowshoe hares throughout a cycle and concluded that animals were restricted largely to islands or foci of favourable habitat during low years but dispersed into less favourable habitats as densities increased. Keith and Surrendi (1971) similarly showed that, following a forest fire, hares abandoned severely burned sites and concentrated in less severely damaged areas. As populations increased, however, hares (particularly young hares) dispersed into surrounding habitats and eventually reoccupied the more marginal areas (which by that time had started to regenerate). Because snowshoe hare populations in the Athabasca region were increasing to or had reached peak population densities, indices of habitat use obtained in this study likely reflect a more widespread use of boreal forest communities. During population lows or declines, the relative importance or quality of these habitats may change as remaining snowshoe hares become more restricted to foci of favourable habitat. It is important then, that any future evaluations of impacts of oil sands developments on snowshoe hare habitat consider the possibility of such changes in habitat use and quality with changes in snowshoe hare abundance.

6.5 CONCLUSIONS

Based on population trends of four snowshoe hare study populations in the Athabasca Basin from July 1978 to January 1980 and regional population trends [as reported by Keith and Windberg (1978)], snowshoe hare populations in northeastern Alberta appeared to be increasing in numbers although peak population sizes may have been reached in 1979-1980. Present information is insufficient, however, to determine the exact status of the snowshoe population cycle in this region.

Comparison of peak population sizes, population trends, levels of reproductive activity, nutritional condition, and indices of dispersal for each of the four study populations indicated that the demographic parameters of these populations differed between study areas (= habitat types). Snowshoe hares populations in black spruce forest habitat appeared to be most characteristic of populations in high quality habitats; populations increased to moderately high numbers each year, reproductive activity was moderate to high, nutritional conditions were average, recruitment of young animals born on the area was high, and most population losses were associated with emigration. In contrast, snowshoe hares in aspen and jack pine communities appeared to be characteristic of animals in marginal (poor quality) habitats; populations tended to be small, reproductive activity was moderate to low, nutritional conditions tended to be average to below average, juvenile recruitment was limited, immigration was moderate to high, and most population losses were associated with increased mortality during the fall and winter periods. Animals on the balsam poplar study area showed some characteristics of animals in both high quality and marginal habitats, suggesting that this habitat was moderately suitable for this species.

Indices of habitat use based on peak population sizes and multivariate analyses of the relationship between snowshoe hare numbers and habitat structure similarly suggested that snowshoe hares selected some habitat types over others. Indices of habitat use implied that black spruce forest habitat was the most important habitat (of the four evaluated) for snowshoe hares in northeastern Alberta, whereas aspen and jack pine forests were marginally suitable habitats; this is identical to the evaluations of these habitats on the basis of population characteristics. Black spruce habitats were associated consistently with the highest peak population sizes and a number of the major vegetation components of black spruce forest (e.g., *P. mariana, L. laricina, Salix* spp., *L. groenlandicum*) were correlated significantly with higher numbers of snowshoe hares during the summer and winter periods. In contrast, jack pine and aspen communities consistently supported the smallest number of animals in each year and a number of the shrub and ground cover components of these habitats were associated significantly with lower numbers of snowshoe hares.

7. SMALL MAMMAL DAMAGE TO WOODY-STEMMED PLANTS

Small mammals (small rodents and snowshoe hares) are capable of damaging large numbers of young trees and shrubs and have been known to restrict afforestation and reforestation programs. Voles of the genus *Microtus* are considered to be one of the major small rodent pests in North America and Europe and have caused extensive losses of orchard and nursery stock by girdling of young trees (Bailey 1924; Littlefield et al. 1946; Jokela and Lorenz 1959; Cayford and Haig 1961; Buckner 1970; Hansson 1975; Larsson 1975; Radvanyi 1978). *Clethrionomys* spp. also have been reported to girdle young trees and shrubs (Gessel and Orians 1967; Black et al. 1969; Hornfeldt 1978) but do not appear to be as severe a pest as *Microtus* spp. Snowshoe hares (*Lepus americanus*) have similarly been known to severely damage young trees in natural situations and in planations by girdling and by browsing (clipping) of terminal and lateral twigs (MacLulich 1937; Aldous and Aldous 1944; Trapp 1962; Black et al. 1969; Keith 1972). Although *P. maniculatus* is not considered a major cause of girdling damage to saplings, evidence from stomach analyses in this study has shown that this species does consume bark from at least one species of shrub (Section 5.3.3). *Peromyscus maniculatus* is one of the major consumers of coniferous seed, however, and is considered to be one of the major causes of failures to re-establish forest cover by artificial seeding (Howard 1950; Jameson 1952; Black 1969; Gashwiler 1969; Radvanyi 1973; Everett et al. 1978; Sullivan 1978).

With the exception of several studies of *L. americanus* and *P. maniculatus*, few studies have assessed the effects of small mammal damage to trees and shrubs in natural situations. In this study, levels of girdling and browsing damage to woody-stemmed plants by small mammals in six of the major forest cover types of the boreal forest ecotone and in two successional areas were assessed over a 2 year period. Effects of seed consumption by *P. maniculatus* on trees and shrubs were not considered in this program. Several aspects of girdling and browsing damage were considered:

1. Do levels of small mammal damage vary among habitats?
2. Are some species of trees and shrubs more susceptible to damage by small rodents and snowshoe hares?
3. Are levels of damage related to the abundance of small mammals? and
4. Are levels of damage associated with vegetation structure?

7.1 SPECIFIC METHODS

Damage by small rodents and snowshoe hares to saplings and shrubs was assessed during the vegetation analyses described in Section 4.1. All tree saplings and shrubs present in the 30 16 m^2 quadrats on each study area were examined for small mammal damage. In 1978, the number of individual plants of each species girdled by rodents or browsed by snowshoe hares was recorded. In 1979, the number of stems damaged by small rodents and snowshoe hares was recorded.

Girdling refers specifically to the removal of the phloem and the outer cambium layers of the stem, roots and/or branches. Damage to these layers was classified as girdling only if rodent teeth marks were visible in the remaining woody tissue. Girdling damage was rated according to the percentage (in 25% increments) of the total circumference of the stem that had been damaged; five girdling classes were recognized: $0\% <$ Class $1 < 25\%$; $25\% \leq$ Class $2 < 50\%$; $50\% \leq$ Class $3 < 75\%$; $75\% <$ Class $4 < 100\%$; and Class 5 = total girdling. Browsing refers to the clipping of terminal and lateral twigs and buds. Browsing and girdling damage was described as old (exposed woody tissue weathered; calloused growth around the wound) or new (exposed woody tissue not weathered).

Because both old and new girdling damage by small rodents rarely was encountered on any study area, a cumulative index of all small rodent damage was calculated for each species of sapling. Old and new rodent girdling was ranked (from 1 = Class 1 damage to 5 = Class 5 damage) and the sum of these girdling ranks for each sample was calculated. The mean cumulative damage for the 30 samples on each study area then was computed for each species of tree and shrub on each study area and will be referred to as a girdling index.

7.2 RESULTS: SMALL RODENT DAMAGE

7.2.1 Small Rodent Damage and Habitat Type

Population characteristics and habitat use of *Microtus pennsylvanicus*, *Clethrionomys gapperi*, and *Peromyscus maniculatus* varied markedly between some habitats (Section 3 and 4). As a result, it is probable that levels of small rodent damage to saplings may vary among habitats as well.

Girdling indices for each species of tree and shrub within each of the 30 sampling plots on each study area were standardized by expressing levels of girdling damage as a girdling index/plant. A girdling index/stem was also obtained in 1979. Girdling indices/stem or girdling indices/plant can range from 0.0, indicating that no plants or stems were girdled, to 5.0, indicating that all stems or plants were totally girdled.

In 1978, girdling damage by small rodents was limited. No girdling damage to any species of tree or shrub was observed on the Jack Pine, Balsam Poplar, or Thickwood Cutline study areas (Tables 28 to 35). Traces (girdling index < 0.001/plant) of girdling damage were recorded on the Aspen and Poplar Creek Cutline study areas. Several species of trees and shrubs showed very low levels of girdling damage (girdling indices ranged from traces to 0.124/stem) on the Willow, Black Spruce, and Tamarack study areas. A comparison of the total girdling damage for all trees and shrubs combined on each study area indicated that girdling damage varied significantly among different habitats (one-way ANOVA: F = 3.25; 7,232 df; P = 0.003); damage was significantly greater (P = 0.05; Student-Neuman-Keuls procedure) on the Tamarack study area than on the Aspen, Jack Pine, Balsam Poplar, Poplar Creek Cutline, or Thickwood Cutline study areas.

Table 28. Summary of small mammal damage on the Aspen study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

			Small Rodent Damage		Snowshoe Hare Damage	
Species	# Plants/ha	# Stems/ha	# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. tremuloides	1354 ± 298		0	0	0	63 ± 56
P. glauca	1125 ± 410		0	0	0	trace
Salix spp.	333 ± 136		0	0	0	63 ± 63
B. glandulosa	21 ± 21		0	0	0	0
Alnus spp.	125 ± 106		0	0	0	125 ± 88
A. alnifolia	23 417 ± 2115		21 ± 21	trace	0	2313 ± 569
P. pensylvanica	21 ± 21		0	0	0	0
Rosa spp.	7083 ± 674		0	0	0	375 ± 106
S. canadensis	4438 ± 595		21 ± 21	trace	63 ± 31	500 ± 181
S. albus	3333 ± 619		0	0	0	trace
V. edule	3917 ± 953		0	0	0	0
V. trilobum	3042 ± 1143		0	0	0	0
R. triste	21 ± 21		0	0	0	0
1979						
P. tremuloides	1083 ± 325	1083 ± 325	21 ± 21	0.04 ± 0.04	0	125 ± 88
P. glauca	1313 ± 455	1375 ± 462	0	0	0	0
Salix spp.	1000 ± 330	2063 ± 446	167 ± 116	0.23 ± 0.18	0	625 ± 256
Alnus spp.	21 ± 21	250 ± 250	0	0	0	125 ± 106
A. alnifolia	22 688 ± 2365	26 021 ± 2736	813 ± 599	0.10 ± 0.07	1188 ± 400	3000 ± 694
Rosa spp.	15 083 ± 1791	15 208 ± 1811	208 ± 157	0.08 ± 0.06	563 ± 400	500 ± 213
S. canadensis	2271 ± 617	11 146 ± 2790	63 ± 63	0.02 ± 0.02	0	375 ± 275
S. albus	4125 ± 595	4208 ± 586	0	0	trace	125 ± 75
V. edule	3313 ± 1157	3396 ± 1193	0	0	125 ± 106	0
R. melanolasius	4604 ± 2013	4771 ± 2060	21 ± 21	trace	125 ± 125	0

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Table 29. Summary of small mammal damage on the Jack Pine study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

Species	# Plants/ha	# Stems/ha	Small Rodent Damage		Snowshoe Hare Damage	
			# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. tremuloides	8625 ± 1064		0	0	0	2563 ± 525
P. glauca	354 ± 133		0	0	0	0
P. banksiana	63 ± 46		0	0	0	0
Salix spp.	1479 ± 380		0	0	trace	313 ± 138
B. glandulosa	667 ± 347		0	0	0	188 ± 94
Alnus spp.	854 ± 495		0	0	0	750 ± 494
A. alnifolia	6604 ± 2133		0	0	0	63 ± 44
P. pensylvanica	42 ± 42		0	0	0	63 ± 44
Rosa spp.	1583 ± 882		0	0	0	125 ± 125
1979						
P. tremuloides	10 042 ± 1447	10 313 ± 1440	167 ± 112	0.12 ± 0.11	0	2500 ± 544
P. glauca	375 ± 122	396 ± 129	0	0	0	63 ± 44
L. laricina	21 ± 21	21 ± 21	0	0	0	0
P. banksiana	229 ± 132	229 ± 132	0	0	0	0
B. papyrifera	42 ± 42	42 ± 42	0	0	0	0
Salix spp.	1208 ± 422	5792 ± 2167	0	0	188 ± 150	500 ± 231
B. glandulosa	1333 ± 933	3833 ± 1951	167 ± 94	0.02 ± 0.01	1563 ± 856	500 ± 263
Alnus spp.	1167 ± 696	2354 ± 950	42 ± 42	0.01 ± 0.01	500 ± 256	500 ± 381
A. alnifolia	6896 ± 2426	7146 ± 2438	21 ± 21	0.02 ± 0.02	0	1063 ± 444
P. pensylvanica	229 ± 209	229 ± 209	0	0	0	63 ± 44
Rosa spp.	1208 ± 714	1750 ± 884	63 ± 63	0.05 ± 0.05	250 ± 269	63 ± 44

Table 30. Summary of small mammal damage on the Willow study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

Species	# Plants/ha	# Stems/ha	Small Rodent Damage		Snowshoe Hare Damage	
			# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. tremuloides	333 ± 198		42 ± 29	trace	0	63 ± 31
P. balsamifera	42 ± 42		0	0	0	0
P. glauca	63 ± 63		0	0	0	0
P. mariana	875 ± 239		0	0	0	0
Salix spp.	8542 ± 2657		0	0	0	563 ± 125
B. glandulosa	13 771 ± 1312		271 ± 250	trace	trace	3938 ± 456
Rosa spp.	83 ± 83		0	0	0	0
R. oxycanthoides/ hirtellum	21 ± 21		0	0	0	0
1979						
P. tremuloides	458 ± 301	458 ± 301	0	0	0	0
P. glauca	42 ± 42	42 ± 42	0	0	0	0
P. mariana	688 ± 170	688 ± 170	0	0	0	0
Salix spp.	6417 ± 542	68 833 ± 6467	0	0	63 ± 63	3000 ± 769
B. glandulosa	6479 ± 452	54 917 ± 4613	500 ± 171	0.02 ± 0.01	10 500 ± 2694	7688 ± 1250
R. oxycanthoides/ hirtellum	750 ± 250	979 ± 301	0	0	63 ± 44	0

Table 31. Summary of small mammal damage on the Balsam Poplar study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

Species	# Plants/ha	# Stems/ha	Small Rodent Damage: # Plant Units Girdled/ha	Small Rodent Damage: Girdling Index/ Plant Unit	Snowshoe Hare Damage: # Stems Newly Browsed/ ha	Snowshoe Hare Damage: # Stems with Old Browse/ ha
1978						
P. tremuloides	500 ± 154		0	0	0	63 ± 50
P. balsamifera	1063 ± 280		0	0	0	125 ± 63
P. glauca	42 ± 42		0	0	0	0
B. papyrifera	21 ± 21		0	0	0	0
B. glandulosa	5500 ± 1291		0	0	188 ± 188	125 ± 75
Alnus spp.	7521 ± 1576		0	0	trace	2500 ± 888
Rosa spp.	4229 ± 537		0	0	63 ± 63	188 ± 94
C. stolonifera	5708 ± 1202		0	0	63 ± 44	750 ± 213
R. oxyacanthoides/ hirtellum	4063 ± 674		0	0	0	125 ± 94
R. americanum	2208 ± 609		0	0	0	0
V. edule	458 ± 201		0	0	0	0
V. trilobum	2417 ± 602		0	0	0	125 ± 100
R. melanolasius	458 ± 284		0	0	0	trace
R. triste	13 854 ± 1720		0	0	563 ± 213	250 ± 156
1979						
P. tremuloides	146 ± 83	146 ± 83	0	0	0	63 ± 63
P. balsamifera	1000 ± 308	1229 ± 349	104 ± 53	0.26 ± 0.14	0	125 ± 75
P. glauca	21 ± 21	21 ± 21	0	0	0	0
B. glandulosa	10 188 ± 1783	10 188 ± 1783	0	0	0	0
Alnus spp.	6604 ± 1297	8188 ± 1548	42 ± 29	0.01 ± 0.01	1875 ± 613	438 ± 138
A. alnifolia	146 ± 107	229 ± 136	0	0	0	0
P. pensylvanica	42 ± 42	42 ± 42	0	0	0	0
Rosa spp.	5917 ± 1139	8458 ± 1548	167 ± 73	0.10 ± 0.06	2500 ± 488	188 ± 119
C. stolonifera	10 604 ± 2059	13 271 ± 2582	21 ± 21	0.01 ± 0.01	1563 ± 406	250 ± 131
R. oxyacanthoides/ hirtellum	9229 ± 1303	10 292 ± 1455	0	0	750 ± 344	63 ± 81

continued...

Table 31. Concluded.

Species	# Plants/ha	# Stems/ha	Small Rodent Damage		Snowshoe Hare Damage	
			# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
R. americanum	10 125 ± 2688	10 271 ± 2725	0	0	63 ± 44	63 ± 44
S. albus	167 ± 73	167 ± 73	0	0	0	0
V. edule	500 ± 419	500 ± 419	0	0	63 ± 44	63 ± 81
R. melanolasius	3188 ± 1412	3688 ± 1463	0	0	63 ± 56	63 ± 44
R. triste	12 896 ± 1782	22 979 ± 3657	83 ± 58	trace	7813 ± 1794	125 ± 125

Table 32. Summary of small mammal damage on the Poplar Creek cutline study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded onlv in 1979.)

Species	# Plants/ha	# Stems/ha	Small Rodent Damage		Snowshoe Hare Damage	
			# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. tremuloides	271 ± 119		0	0	0	0
P. balsamifera	1417 ± 738		0	0	0	0
P. glauca	63 ± 46		0	0	0	0
B. papyrifera	21 ± 21		0	0	0	0
Salix spp.	3396 ± 646		21 ± 21	trace	0	0
B. glandulosa	583 ± 268		0	0	0	0
Alnus spp.	479 ± 273		0	0	0	0
A. alnifolia	83 ± 83		0	0	0	0
Rosa spp.	6188 ± 1472		0	0	0	0
C. stolonifera	1854 ± 935		0	0	0	0
R. oxyacanthoides/ hirtellum	83 ± 58		0	0	0	0
R. americanum	63 ± 46		0	0	0	0
S. canadensis	42 ± 42		0	0	0	0
S. albus	104 ± 85		0	0	0	0
V. edule	125 ± 76		0	0	0	0
R. melanolasius	1500 ± 852		0	0	0	0
R. triste	2771 ± 1846		0	0	0	0
1979						
P. tremuloides	271 ± 107	292 ± 115	42 ± 29	0.13 ± 0.10	0	0
P. balsamifera	3979 ± 992	4792 ± 1366	146 ± 65	0.05 ± 0.04	0	0
B. papyrifera	375 ± 257	375 ± 257	21 ± 21	trace	0	0
Salix spp.	4521 ± 936	7292 ± 1426	83 ± 50	0.05 ± 0.03	0	0
B. glandulosa	667 ± 563	792 ± 576	0	0	0	0
Alnus spp.	250 ± 118	521 ± 245	0	0	0	0
Rosa spp.	6771 ± 1689	10 146 ± 2578	0	0	0	0
C. stolonifera	292 ± 149	708 ± 373	0	0	trace	0

continued...

Table 32. Concluded.

Species	# Plants/ha	# Stems/ha	Small Rodent Damage: # Plant Units Girdled/ha	Small Rodent Damage: Girdling Index/ Plant Unit	Snowshoe Hare Damage: # Stems Newly Browsed/ ha	Snowshoe Hare Damage: # Stems with Old Browse/ ha
R. oxycanthoides/ hirtellum	42 ± 42	42 ± 42	0	0	0	0
R. americanum	21 ± 21	21 ± 21	0	0	0	0
V. edule	21 ± 21	21 ± 21	0	0	0	0
R. melanolasius	313 ± 292	396 ± 375	0	0	0	0
R. triste	1958 ± 622	3813 ± 1455	21 ± 21	0.10 ± 0.10	0	0

Table 33. Summary of small mammal damage on the Black Spruce study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling damage densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

			Small Rodent Damage		Snowshoe Hare Damage	
Species	# Plants/ha	# Stems/ha	# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. tremuloides	1250 ± 441		292 ± 107	trace	0	625 ± 319
P. balsamifera	42 ± 42		0	0	0	0
P. glauca	813 ± 301		0	0	0	63 ± 31
P. mariana	10 208 ± 1245		0	0	0	188 ± 75
L. laricina	583 ± 153		83 ± 50	trace	0	375 ± 113
B. papyrifera	21 ± 21		0	0	0	0
Salix spp.	7125 ± 2796		0	0	188 ± 81	750 ± 244
B. glandulosa	854 ± 353		83 ± 83	trace	125 ± 88	563 ± 250
Rosa spp.	3521 ± 1223		0	0	0	125 ± 75
R. oxyacanthoides/ hirtellum	21 ± 21		0	0	0	0
S. canadensis	42 ± 29		0	0	0	0
1979						
P. tremuloides	1646 ± 599	1958 ± 620	479 ± 189	0.27 ± 0.10	0	438 ± 163
P. balsamifera	208 ± 125	208 ± 125	0	0	0	63 ± 48
P. glauca	208 ± 208	208 ± 208	0	0	0	0
P. mariana	10 479 ± 1500	10 479 ± 1500	0	0	0	63 ± 31
L. laricina	813 ± 273	896 ± 284	21 ± 21	0.01 ± 0.01	0	375 ± 100
B. papyrifera	167 ± 167	167 ± 167	0	0	0	63 ± 63
Salix spp.	1271 ± 508	6042 ± 3099	63 ± 63	0.01 ± 0.01	250 ± 175	625 ± 369
B. glandulosa	750 ± 624	1396 ± 910	21 ± 21	trace	813 ± 575	250 ± 200
Alnus spp.	63 ± 46	1021 ± 744	0	0	688 ± 669	625 ± 606
Rosa spp.	2021 ± 878	2021 ± 878	0	0	188 ± 113	188 ± 100
S. canadensis	63 ± 63	63 ± 63	0	0	trace	0

Table 34. Summary of small mammal damage on the Thickwood Cutline study area in 1978 and 1979. (Means and 1 S.E. of the 30 samples on each study area in each year are shown for tree and shrub densities, girdling densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

			Small Rodent Damage		Snowshoe Hare Damage	
Species	# Plants/ha	# Stems/ha	# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. tremuloides	1396 ± 479		0	0	0	0
P. balsamifera	208 ± 135		0	0	0	0
A. balsamea	21 ± 21		0	0	0	0
Salix spp.	604 ± 145		0	0	0	0
B. glandulosa	625 ± 424		0	0	0	0
Alnus spp.	167 ± 79		0	0	0	0
Rosa spp.	8521 ± 2630		0	0	0	0
R. americanum	21 ± 21		0	0	0	0
R. triste	3083 ± 1117		0	0	0	0
1979						
P. tremuloides	2875 ± 852	3083 ± 902	146 ± 71	0.05 ± 0.03	0	63 ± 31
P. balsamifera	938 ± 938	938 ± 938	0	0	0	0
P. glauca	21 ± 21	21 ± 21	0	0	0	0
B. papyrifera	42 ± 29	42 ± 29	0	0	0	0
Salix spp.	1125 ± 283	2708 ± 711	21 ± 21	0.01 ± 0.01	trace	0
B. glandulosa	188 ± 104	1792 ± 1053	0	0	0	0
Alnus spp.	146 ± 58	625 ± 300	0	0	0	0
Rosa spp.	8813 ± 2571	16 146 ± 3733	0	0	63 ± 44	0
R. oxycanthoides/ hirtellum	625 ± 604	625 ± 604	0	0	0	0
R. americanum	688 ± 624	688 ± 624	0	0	0	0
R. triste	11 438 ± 2351	27 500 ± 4802	21 ± 21	trace	63 ± 50	0

Table 35. Summary of small mammal damage on the Tamarack study area in 1978 and 1979. (Means and 1 S.E. are shown for tree and shrub densities, girdling damage densities, girdling indices, and hare damage. Units in 1978 were plants. Units in 1979 were stems. The numbers of stems/ha were recorded only in 1979.)

			Small Rodent Damage		Snowshoe Hare Damage	
Species	# Plants/ha	# Stems/ha	# Plant Units Girdled/ha	Girdling Index/ Plant Unit	# Stems Newly Browsed/ ha	# Stems with Old Browse/ ha
1978						
P. glauca	1604 ± 1397		0	0	0	0
P. mariana	2042 ± 515		0	0	0	375 ± 131
L. laricina	4875 ± 597		42 ± 42	trace	0	2250 ± 388
A. balsamea	21 ± 21		0	0	0	0
B. papyrifera	125 ± 87		21 ± 21	trace	0	0
Salix spp.	3917 ± 1012		0	0	188 ± 100	938 ± 350
B. glandulosa	14 708 ± 2446		688 ± 240	trace	1688 ± 613	9000 ±1931
1979						
P. glauca	333 ± 333	333 ± 333	0	0	0	0
P. mariana	5792 ± 2790	5813 ± 2789	21 ± 21	0.08 ± 0.08	0	313 ± 156
L. laricina	6000 ± 1034	6417 ± 1026	250 ± 98	0.16 ± 0.07	0	1500 ± 344
B. papyrifera	83 ± 83	875 ± 875	0	0	0	0
Salix spp.	4833 ± 882	14 292 ± 3042	125 ± 76	0.02 ± 0.02	5375 ± 1375	2500 ± 844
B. glandulosa	8792 ± 1160	89 250 ± 13 256	3167 ± 811	0.13 0.04	85 750 ± 15 313	16 250 ± 3600

In 1979, girdling damage to shrubs and trees was also limited (Tables 28 to 35). Traces of girdling damage were recorded on the Willow, Poplar Creek Cutline, and Thickwood Cutline study areas, whereas very low levels of damage were observed on the Aspen, Jack Pine, Balsam Poplar, Black Spruce, and Tamarack study areas. However, differences among habitats in the total amount of girdling damage to all species of trees and shrubs combined were not significant (one-way ANOVA: $F = 1.56$; 7,232 df; $P = 0.15$).

Levels of girdling damage by small rodents on each study area also varied significantly between years ($F = 11.70$; 1,479 df; $P < 0.001$). Levels of old and new damage combined to woody-stemmed plants increased significantly between 1978 and 1979. However, only 2.3% of the variance in the levels of small rodent damage to trees and shrubs on the eight study plots over the two years of the study, was accounted for by differences between the two years (multiple classification analysis, Nie et al. 1975). Differences among study areas within each year accounted for 8.4% of the total variance. This suggests that vegetation communities and small mammal populations associated with these habitats are more important influences on levels of small rodent damage than changes in habitat or in small mammal populations between years.

7.2.2 Susceptibility of Trees and Shrubs to Small Rodent Damage

Small rodents have been shown to preferentially damage some species of trees and shrubs (Littlefield et al. 1946; Jokela and Lorenz 1959; Cayford and Haig 1961; Sartz 1970; Von Althen 1971). Preferences of small rodents in the Athabasca region were assessed by comparing the availability of each tree and shrub species, (i.e., mean density of that species) to the mean number of plants and stems of that species girdled by small mammals (old and new damage were included in this mean). Only species damaged by small rodents were included in the analysis for each year. Species not damaged were obviously less commonly damaged than species included in the analyses. Because the clustered distributions of shrub stems may influence levels of damage, separate analyses were conducted for trees and for shrubs.

In both 1978 and 1979, several species of trees sustained disproportionate amounts of damage (1978: $\chi^2 = 77.3$; 2 df; $P < 0.001$; 1979: $\chi^2 = 501.9$; 4 df; $P < 0.001$) (Table 36). In 1978, *Betula papyrifera* was most susceptible to damage by small rodents, whereas *Larix laricina* was least susceptible. In 1979, *Populus tremuloides*, *Populus balsamifera*, and *L. laricina* sustained heavier amounts of damage than expected, whereas levels of damage to *Picea mariana* were lower than expected.

Although girdling of shrubs by small rodents was limited in 1978 and 1979, some species of shrubs were more susceptible to damage than other (1978: $\chi^2 = 1424.8$; 2 df; $P < 0.001$; 1979: $\chi^2 = 2921.6$; 8 df; $P < 0.001$) (Table 36). In 1978, *Amelanchier alnifolia* was most susceptible to girdling, whereas *Salix* spp. and *Betula glandulosa* received less damage than expected.

In 1979, however, *B. glandulosa* and *A. alnifolia* were more prone to girdling, whereas damage to *Salix* spp., *Alnus* spp., *Rosa* spp., *Cornus stolonifera*, *Shepherdia canadensis*, *Rubus melanolasius*, and *Ribes triste* were significantly lower than expected.

7.2.3 Small Rodent Damage and Population Size

An implicit but as yet unconfirmed assumption of the use of rodenticides, chemosterilants, and several other techniques for the control of small rodent damage to plants [see Green (1978) for a review] is that levels of damage are related directly to the size of the pest population. Regression analyses were used in this study to assess the relationship between the abundance of small rodents and levels of girdling damage to trees and shrubs in natural areas. The number of captures per trap-night (CTN) was used as an index of abundance for each small rodent species in each of the 30 vegetation sampling quadrats on each study area during the summers of 1978 and 1979 and the winter of 1978 to 1979; methods for calculating CTN are described more fully in Section 4.3. Summer CTN for 1978 included all captures between 1 July and 27 August 1978; the summer CTN for 1979 included all captures between 24 June and 31

Table 36. Susceptibility of naturally occurring species of trees and shrubs to small rodent damage. [Significant differences between observed levels of damage and levels of damage expected based on the availability of that species are based on a Bonferroni z-test with a 95% confidence interval (Neu et al. 1974).]

	Small Rodent Girdling		Hare Damage			
			1978		1979	
Species	1978	1979	New	Old	New	Old
Trees						
P. tremuloides	0[a]	+	ND	+	ND	+
P. balsamifera	ND	+	ND	-	ND	-
P. glauca	ND	ND	ND	-	ND	ND
P. mariana	ND	-	ND	-	ND	-
L. laricina	-	+	ND	+	ND	+
P. banksiana	ND	ND	ND	ND	ND	+
B. papyrifera	+	0	ND	ND	ND	ND
Shrubs						
Salix spp.	-	-	-	-	-	-
B. glandulosa	-	+	+	+	+	+
Alnus spp.	ND	-	ND	+	-	+
A. alnifolia	+	+	ND	-	-	+
P. pensylvanica	ND	ND	ND	+	ND	0
Rosa spp.	ND	-	-	-	-	-
C. stolonifera	ND	-	-	-	-	-
R. oxycanthoides/hirtellum	ND	ND	ND	-	-	-
R. americanum	ND	ND	ND	ND	-	-
S. canadensis	ND	-	-	-	ND	ND
L. dioica	ND	ND	ND	ND	ND	ND
S. albus	ND	ND	ND	ND	ND	-
Viburnum spp.	ND	ND	ND	-	-	-
R. melanolasius	ND	-	ND	ND	-	-
R. triste	ND	-	+	-	-	-

[a] Levels of damage related to the availability of that species.

ND	no damage recorded = most resistant
0	damage not significantly different from availability = resistant
-	damage significantly lower than expected from availability = susceptible
+	damage significantly higher than availability = most susceptible

August 1979; and the winter CTN for 1978 to 1979 included all captures between 27 October 1978 and 16 May 1979. Estimates of the girdling index/plant and of the girdling index/stem for all trees and shrubs (occurring in each vegetation plot) combined were used as indices of small rodent damage in 1978 and 1979, respectively.

During the summer of 1978, amounts of damage to trees and shrubs were negatively associated with the abundance of *C. gapperi* ($r = 0.11$; $b = -10.63$; $P = 0.05$; $N = 240$) and of *P. maniculatus* ($r = 0.13$; $b = -11.14$; $P = 0.02$; $N = 240$) but were positively associated with the numbers of *M. pennsylvanicus* ($r = 0.13$; $b = 12.54$; $P = 0.03$; $N = 240$). Although these relationships were statistically significant, changes in small rodent abundance explained only 1.1 to 1.7% of the variance in small rodent damage, indicating that population sizes of small rodents during the summer 1978 were a minor influence on amounts of damage.

Amounts of girdling damage to trees and shrubs in 1979 were negatively associated with the numbers of *M. pennsylvanicus* ($r = 0.12$; $b = -5.12$; $P = 0.03$; $N = 240$) and of *P. maniculatus* ($r = 0.11$; $b = -10.44$; $P = 0.04$; $N = 240$) during the summer months but were not significantly related with the abundance of *C. gapperi* ($r = -0.09$; $b = 5.36$; $P = 0.07$; $N = 240$). Relationships between small rodent abundance and amounts of damage again explained only a small amount of the variance in small rodent damage (1.3 to 1.4%).

A number of studies have suggested that girdling of trees and shrubs by small rodents occurs predominantly during the winter months [see Myllymaki (1975a) for a review]; shortages of forage of adequate nutritional quality during the winter period apparently are associated with increased consumption of bark (Bailey 1924; Hansson 1973a). Regression analyses were used to assess the relationship between the winter abundance of small rodents and amounts of damage. Levels of small rodent damage to trees and shrubs observed during the summer of 1979 were assumed to be representative of damage caused during the winter of 1978 to 1979. Winter abundance of small rodents was estimated using the total CTN for the last two trapping periods in the late fall of 1978 and the first trapping period (May 6) in 1979.

Levels of girdling damage were not significantly related with numbers of small rodents during the winter of 1978 to 1979 (*C. gapperi*: $r = 0.06$; $b = -0.04$; $P = 0.17$; $N = 240$; *M. pennsylvanicus*: $r = 0.01$; $b = 0.01$; $P = 0.43$; $N = 240$; *P. maniculatus*: $r = 0.08$; $b = -0.04$; $P = 0.12$; $N = 240$).

7.2.4 Small Mammal Damage and Habitat Structure

Previous studies of small mammal damage to saplings and shrubs have suggested that components of habitat structure, such as the density of ground cover, the abundance and diversity of food types, and the density of trees and shrubs, can influence levels of small rodent damage to plants (Eadie 1953; Jodela and Lorenz 1959; Howard 1967; Buckner 1970). Two aspects of the relationship between habitat structure and amounts of damage were examined in this study; a regression analysis of the relationship between tree and shrub densities and amounts of damage, and a multivariate analysis of the relationships between habitat structure and levels of girdling damage.

7.2.4.1 Plant densities and damage. The relationship between plant densities and girdling damage was assessed using the total numbers of plants (in 1978) and stems (in 1979) and the girdling index for all trees and shrubs combined for each vegetation sampling quadrat (16 m^2). Plant densities were not significantly correlated with girdling damage in 1978 ($r = 0.03$; $b = 0.14$; $P = 0.34$; $N = 240$). In 1979, however, stem densities were significantly and positively correlated with small rodent damage ($r = 0.26$; $b = 1.09$; $P < 0.001$). The relationship be between stem densities and girdling damage was weak, however, and explained only 6.8% of the total variance in small rodent damage.

7.2.4.2 Habitat structure and girdling damage. There were two steps in the multivariate assessment of the relationships between indices of small rodent damage and vegetation structure. Initially, a factor analysis was used to reduce a larger number of habitat variables to a small number of independent factors that characterized vegetation structure on the eight live-trapping areas (see Section 4.3). Stepwise multiple regression analyses (SMR) (BMDP2R; Dixon and Brown 1979) then were used to assess and quantify the relative importance of each factor in predicting amounts of damage by small rodents. Habitat factors were allowed to enter the SMR model only if F-ratios exceeded 3.0. Estimates of damage were transformed using the square root (x + 1) (where x is the damage estimate for that sample) to correct for non-normality (Sokal and Rolf 1969).

In 1978, only 15% of the variation in levels of mouse damage was explained by habitat structure (Table 37). Aspen understory and jack pine understory were positively correlated with levels of girdling damage, whereas balsam poplar understory, *Viburnum* shrub cover, and *Equisetum* cover were all negatively correlated. Aspen understory and the *Viburnum* shrub cover were the most important predictor variables, explaining 5.9 and 4.3% of variation in levels of damage, respectively.

In 1979, differences in habitat structure were associated with only 5% of the variance in girdling damage (Table 38). Higher levels of damage were associated most commonly with successional habitat, whereas lower levels of damage were associated with *Viburnum* shrub cover and jack pine understory. The successional cover, *Viburnum* shrub cover, and jack pine understory factors accounted for 1.9, 1.9, and 1.2% of the total variance in damage, respectively.

7.3 RESULTS: SNOWSHOE HARE DAMAGE

7.3.1 Snowshoe Hare Damage and Habitat Type

Based on the results of this study and several recent studies of snowshoe hare populations (Dolbeer and Clark 1975; Wood and Munroe 1977; Keith and Windberg 1978), it is apparent that snowshoe hares show distinct habitat preferences and that some population characteristics vary with habitat type. Keith (1972) also showed that levels of damage to trees and shrubs by snowshoe hares varied according to the vegetation composition of the community.

Table 37. SMR analysis of the levels of damage by small rodents in 1978. (See Table 17 for explanation of factor names. $R^2 = 0.15$; 1 S.E. of the transformed estimate = 0.06; $F = 8.36$; df = 5,234; $P < 0.001$.)

Factor Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P[a]
Constant		1.012				
Aspen understory	1	0.015	0.004	0.0587	0.587	***
Viburnum shrub cover	2	-0.012	0.005	0.1018	0.0432	***
Balsam poplar understory	3	-0.009	0.005	0.1252	0.0233	**
Jack pine understory	4	0.015	0.004	0.1394	0.0143	***
Equisetum cover	5	0.007	0.004	0.1515	0.0121	**

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 38. SMR analysis of the levels of damage by small rodents in 1979. (See Table 17 for explanation of factor names. $R^2 = 0.05$; 1 S.E. of the transformed estimate = 0.09; $F = 4.17$; df = 3,236; $0.01 > P > 0.001$.)

Factor Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		1.028				
Young successional	1	-0.009	0.005	0.0191	0.0191	**
Dwarf birch shrub	2	0.013	0.006	0.0380	0.0190	**
Jack pine understory	3	-0.012	0.005	0.0504	0.0123	*

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, $P \geq 0.001$.

In 1978, amounts of old browse on trees differed significantly among habitats (one-way ANOVA: $F = 16.32$; 7,232 df; $P < 0.001$). Amounts of old damage were significantly lower on the Poplar Creek Cutline, Thickwood Cutline, Willow, Jack Pine, and Balsam Poplar study areas than on the Black Spruce, Aspen, or Tamarack study areas (Student-Newman-Keuls procedure; $P = 0.05$) (Tables 28 to 35). In contrast, old damage on the Aspen and Tamarack study areas was significantly higher than on any other study area.

Levels of both old and new snowshoe browse on shrubs were also significantly related to habitat (new damage: $F = 7.57$; 7,232 df; $P < 0.001$; old damage: $F = 14.98$; 7,232 df; $P < 0.001$). Both old and new damage was significantly more severe on the Tamarack study area than on the remaining seven areas, whereas old damage on the Poplar Creek Cutline and Thickwood Cutline study areas was significantly lower than on most other areas (damage tended to be higher on the Aspen and Black Spruce study areas than on the successional areas but these differences were not significant). Overall, trees and shrubs on the Tamarack study area consistently sustained significantly greater damage than in any other habitat type. Conversely, browsing of trees and shrubs on both successional study areas was significantly less than in most natural habitats.

Very similar trends in snowshoe hare damage to trees and shrubs in each habitat type were observed in 1979. Amounts of damage to trees and shrubs differed significantly among study areas (old damage to trees: $F = 13.84$; 7,232 df; $P < 0.001$; new damage to shrubs: $F = 30.94$; 7,232 df; $P < 0.001$; old damage to shrubs: $F = 18.90$; 7,232 df; $P < 0.001$). Old browse damage to trees on the Aspen and Tamarack study areas was significantly higher than on the remaining six study areas (Tables 28 to 35). Similarly, old and new browsing of shrubs on the Tamarack study area was significantly more common than in other habitats. Amounts of old browse on shrubs in the Willow study area in 1979 were also significantly greater than in the successional, aspen, jack pine, balsam poplar, or black spruce communities.

Inter-year comparisons of snowshoe hare browse indicated that amounts of damage (old and new combined) to trees did not change significantly between years ($F = 1.10$; 1,479 df; $P = 0.30$)[1]. Differences in the amounts of damage between years accounted for only 1.6% of the variation in browsing damage, whereas inter-habitat differences explained 36.4%. Browse damage to shrubs on each area, however, increased significantly between years ($F = 55.91$; 1,479 df; $P < 0.001$). Differences in browse damage between years accounted for 5.8% of the variation in levels of damage, whereas inter-habitat differences were associated with 28.5%.

7.3.2 Susceptibility of Trees and Shrubs to Snowshoe Hare Damage

Snowshoe hares utilize a wide range of woody plants but appear to show distinct preferences and avoidances of some browse species (de Vos 1964; Hansen and Flinders 1969; Keith 1972; Klein 1977); food preferences appear to be related partially to the nutritive value of plant parts consumed (Miller 1968; Lindlof et al. 1974) and the availability of each species (de Vos 1964; Telfer 1972). Preferences of snowshoe hares in the Athabasca Basin for trees and shrubs were assessed by comparing the availability of a species (i.e., the number of stems or plants/ha) to the number of stems browsed. Because distributions of shrub stems are more clumped than that of trees, browse damage to trees and shrubs was analysed separately.

In 1979, several tree species were more susceptible to browse damage than others (only old damage was recorded) (1978: $\chi^2 = 5059.5$; 4 df; $P < 0.001$; 1979: $\chi^2 = 3360.9$; 4 df; $P < 0.001$) (Table 36). In both years, *P. tremuloides* and *L. laricina* were most susceptible to damage, whereas *P. balsamifera* and *P. mariana* were were less commonly damaged than expected.

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[1] For comparisons between years, all estimates of the number of stems damaged/vegetation plot in 1979 were converted to the number of plants damaged/vegetation plot by dividing by the average numbers of stems per plant for each species.

New snowshoe hare damage to shrubs in 1978 and 1979 also was not proportionate to the availability of these species (1978: $\chi^2 = 2146.4$; 5 df; $P < 0.001$; 1979: $\chi^2 = 116\ 151.0$; 10 df; $P < 0.001$) Table 36). During both years, *B. glandulosa* and *R. triste* were the most highly preferred browse species and consequently were most susceptible to new damage by snowshoe hares. In contrast, *P. pensylvanica, Lonicera* spp., and *S. albus* were consistently avoided.

Estimates of old damage to shrubs similarly indicated that some species of shrubs were more commonly browsed than others (1978: $\chi^2 = 25\ 087.6$; 10 df; $P < 0.001$; 1979: $\chi^2 = 20\ 535.5$; 12 df; $P < 0.001$) (Table 36). Based on estimates of old damage in each year, *B. glandulosa* and *Alnus* spp. were highly preferred and *P. pensylvanica* and *A. alnifolia* were moderately preferred over most other shrub species, and consequently, were most susceptible to damage. Conversely, *Lonicera* spp., *R. americanum, S. albus, R. melanolasius,* and *S. canadensis* frequently were not browsed and would appear to be the most resistant species to browse damage.

7.3.3 Levels of Snowshoe Hare Damage and Population Size

Pease et al. (1979) observed that browsing intensity of woody stems in natural communities by snowshoe hares became more severe during snowshoe hare population increases and decreased following the population decline. Surveys of browse during the peak winter indicated that over 50% of the woody stems had been severely or heavily browsed. To assess effects of snowshoe hare population sizes on amounts of browse damage during this study, mid-winter population sizes of snowshoe hares on each of the four snowshoe hare study areas in late February to March 1979 were compared to estimates of the mean amounts of old and new browse damage to trees and shrubs on the corresponding small rodent study area (each snowshoe hare study plot encompassed the small rodent trapping area in that habitat type).

Although amounts of old browse damage to shrubs and trees were not significantly related to the numbers of snowshoe hares present during mid-winter (old damage to trees: $r = 0.05$; $b = 7.44$;

$N = 4$; $P = 0.47$; old damage to shrubs: $r = 0.34$; $b = -37.51$; $N = 4$; $P = 0.33$), new damage to shrubs tended to be positively associated with mid-winter population sizes ($r = 0.79$; $b = 41.3$; $N = 4$; $P = 0.10$). This suggests that, during the winter of 1978 to 1979 when snowshoe hare populations were believed to be increasing (see Section 6.4.1), amounts of browsing by snowshoe hares on shrubs were determined partly by the number of animals present in the area.

7.3.4 Snowshoe Hare Damage and Habitat Structure

Keith (1972) conducted a survey of snowshoe damage to woody plants in northern Alberta and concluded that amounts of hare browsing were related directly to the quality of the surrounding community as hare habitat. In addition, studies by de Vos (1964) and Telfer (1972) have suggested that availability is a major determinant of browsing preferences in local areas. Such evidence suggests that habitat structure may directly influence browsing pressures by snowshoe hares.

7.3.4.1 Plant densities and levels of girdling damage. Effects of stand densities on the amounts of snowshoe hare damage to trees and shrubs were assessed by comparing the number of plants (in 1978) and stems (in 1979) damaged with the density of plants or stems in each vegetation sampling quadrat. Density and damage estimates for all species of trees and for all species of shrubs were pooled for the analysis.

In 1978, amounts of old and new damage were significantly associated with plant densities (old damage to trees: $r = 0.39$; $b = 19.19$; $N = 240$; $P < 0.001$; old damage to shrubs: $r = 0.14$; $b = 8.20$; $N = 240$; $P < 0.001$; new damage to shrubs: $r = 0.09$; $b = 20.00$; $N = 240$; $P = 0.008$). Amounts of old damage to trees and old and new damage to shrubs in 1979 were also significantly associated with stem densities (old damage to trees: $r = 0.40$; $b = 27.2$; $N = 240$; $P < 0.001$; new damage to shrubs: $r = 0.27$; $b = 5.78$; $N = 240$; $P < 0.001$; old damage to shrubs: $r = 0.24$; $b = 21.50$; $N = 240$; $P < 0.001$). In both years, greater amounts of damage were associated with higher densities of trees and shrubs.

7.3.4.2 Habitat structure and damage by snowshoe hares.

Multivariate analyses of the relationship between snowshoe hare damage and habitat structure were similar to those described for small rodent damage (Section 7.2.4.2). Estimates of snowshoe hare browse were transformed using a log transformation of the (damage estimate + 1) to correct for non-normality (Sokal and Rolf 1969).

In 1978, 50% of the variation in the levels of browse damage by snowshoe hares was associated with habitat structure (Table 39). The aspen understory, tamarack understory, grass/sedge cover, dwarf-birch shrub, raspberry shrub, willow-birch scrub, and dogwood shrub factors were positively associated, whereas the balsam poplar understory, white spruce understory, rose understory, and *Equisetum* cover factors were negatively associated with levels of browse damage. The aspen understory, balsam poplar understory, and tamarack understory factors were the most important predictor variables, accounting for 14.2, 12.8, and 8.2% of the total variation in browse damage, respectively.

Habitat factors explained 48% of the variation in levels of snowshoe hare damage in 1979 (Table 40). High levels of damage were most commonly associated with the tamarack understory, black spruce forest, dense vertical cover, and successional cover factors, whereas damage was limited in areas dominated by willow-birch scrub, dwarf birch scrub, aspen understory, and white spruce understory. Tamarack understory was the single most important predictor variable (according for 30.9% of the variance in damage).

7.4 DISCUSSION

Damage by small mammals to woody-stemmed plants in natural areas is primarily a problem of feeding behaviours. Browsing damage by snowshoe hares to naturally occurring species of trees and shrubs in the AOSERP study area was encountered more frequently than was girdling damage by small rodents. This is not unexpected; the fall and winter diets of snowshoe hares is composed almost entirely of hardwood browse and the bark and needles of coniferous

Table 39. SMR analysis of the levels of damage by snowshoe hares in 1978. [See Table 17 for explanations of factor names. $R^2 = 0.50$; 1 S.E. of the transformed estimate = 0.38; $F = 20.73$; df = 11,228; $P < 0.001$. All factors were significantly ($P < 0.001$) associated with levels of browse damage.]

Factor Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. for Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor
Constant		0.595			
Aspen understory	1	0.197	0.024	0.1421	0.1421
Balsam poplar understory	2	-0.232	0.028	0.2705	0.1284
Tamarack understory	3	0.185	0.027	0.3529	0.0823
Grass/sedge cover	4	0.050	0.025	0.3908	0.0380
Dwarf birch shrub	5	0.066	0.026	0.4229	0.0320
White spruce understory	6	-0.066	0.026	0.4477	0.0248
Raspberry shrub	7	0.105	0.027	0.4613	0.0136
Rose understory	8	-0.041	0.023	0.4761	0.0148
Willow birch scrub	9	0.086	0.024	0.4844	0.0083
Equisetum cover	10	-0.049	0.025	0.4928	0.0084
Dogwood shrub	11	0.094	0.028	0.5000	0.0072

Table 40. SMR analysis of the levels of damage by snowshoe hares in 1979. [See Table 17 for explanation of factor names. $R^2 = 0.48$; 1 S.E. of the transformed estimate = 0.56; $F = 27.16$; df = 8,231; $P < 0.001$. All factors were significantly ($P < 0.001$) associated with levels of browse damage.]

Factor Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor
Constant	1	0.877			
Tamarack understory	1	0.111	0.038	0.3091	0.3091
Willow/birch scrub	2	-0.129	0.035	0.3493	0.0402
Dwarf birch shrub	3	-0.099	0.043	0.3911	0.0418
Black spruce forest	4	0.397	0.036	0.4274	0.0362
Aspen understory	5	-0.149	0.038	0.4513	0.0240
White spruce understory	6	-0.074	0.037	0.4653	0.0139
Dense vertical cover	7	0.035	0.035	0.4757	0.0104
Successional cover	8	0.035	0.035	0.4847	0.0009

trees (MacLulich 1937; Dodds 1960; Trapp 1962; de Vos 1964; O'Farrell 1965; Klein 1977; Wolff 1978), whereas twigs and bark are minor components of microtine and cricetine diets (Criddle 1932; Hamilton 1941; Dyke 1971; Hansson 1971; Zemanek 1972; Larsson and Hansson 1977; this study).

Feeding behaviours of small mammals appear to be influenced by a number of factors, including forage availability, forage quality, and feeding preferences (e.g., Dyke 1971; Hansson 1971; Telfer 1972; Grant 1978; Wolff 1978). Because girdling damage and browse damage (i.e., the consumption of bark and twigs) are specific types of feeding responses which, under certain circumstances are deemed undesirable by humans, levels and types of small mammal damage are probably influenced by these factors as well.

7.4.1 Damage by Small Rodents

Girdling damage by small rodents has been shown to result in increases in seedling mortality in natural communiites and in reforestation areas (Moore 1940; Staebler et al. 1954; Jokela and Lorenz 1959; Bang 1975; Christiansen 1975; Larsson 1975; Myllymaki 1975a, 1975b). Girdling appears to occur most often during the late fall and winter, but is not necessarily restricted to these periods, and occurs more frequently during periods when small rodent populations are at a peak (Jokela and Lorenz 1959; Hansson 1973a; Myllymaki 1975a).

In natural habitats in the Athabasca Basin, several species of trees and shrubs sustained proportionately higher levels of damage than expected. Two tree species, *P. tremuloides* and *B. papyrifera*, and two shrub species, *B. glandulosa* and *A. alnifolia*, were significantly more susceptible to girdling damage than other species of trees and shrubs. *Picea glauca*, *P. banksiana*, and a number of shrub species such as *P. pensylvanica, Ribes* spp., *Lonicera* spp., *S. albus*, and *Viburnum* spp. sustained no girdling damage in either year of study. No previous studies have assessed small rodent damage to shrub species in natural communities but studies of girdling damage to a number of tree species throughout

North America have suggested, as in this study, that *P. glauca* is avoided by small rodents (Littlefield et al. 1946; Cayford and Haig 1961; Buckner 1970; Sartz 1970; Von Althen 1971). Littlefield et al. (1946) also noted that *P. banksiana* was avoided by small rodents. In contrast, *P. banksiana* in some localities have sustained high levels of girdling damage (Sartz 1970; Buckner 1970; Von Althen 1971). Conflicting results such as these likely reflect local influences of habitat structure, forage availability, and the nutritional condition of the animals on feeding preferences.

In this study, differences among habitats accounted for more of the variation in the amount of small rodent damage than did differences between years, suggesting that the amount of girdling damage was associated largely with physical and biotic differences among habitats. This is in agreement with several studies of the relationship between components of habitat structure and girdling damage. Levels of small rodent damage to trees have been shown to be related closely to the density of ground cover (Jokela and Lorenz 1959; Cayford and Haig 1961), density of trees and shrubs (Buckner 1970), slope aspect (Sartz 1970), and forage availability and quality (Hansson 1973a, 1973b). Multivariate analyses of vegetation structure and damage within the major forest habitats of the Athabasca region, however, failed to reveal any strong statistical relationships. This suggests that the habitat structure of these communities (as measured in this study) was a minor influence on the distribution and extent of girdling damage.

Longer term changes in habitat structure and associated changes in small rodent species diversity and abundance, however, may affect levels of girdling damage. For example, changes in the species composition of small rodent populations that are associated with successional processes in disturbed areas (Sims and Buckner 1973; Krefting and Ahlgren 1974; Lovejoy 1975; Hooven and Black 1976) can influence the relative abundance of small rodent species known to damage trees and shrubs and so influence levels of damage.

Apparent increases in the amount of girdling damage during small mammal population peaks (Jokela and Lorenz 1959; Hansson 1973a; Myllymaki 1975a) suggest that levels of small rodent damage are related directly to the number of mice. Although little evidence is available to suggest that this is the case, a number of methods of controlling small rodent damage have assumed implicitly that reductions in the number of mice will result in a reduction of the amounts of damage (e.g., Smith and Aldous 1947; Peoples 1970; Gratz 1973; Lund 1975; Radvanyi 1978). In this study, levels of small rodent damage in six natural community types and in two successional areas were weakly associated with both summer and winter population sizes of *C. gapperi* and *M. pennsylvanicus*. Because populations of *C. gapperi* and *M. pennsylvanicus* declined between 1978 and 1979, a wide range of population sizes was observed over the two years of this study--the poor association between damage and small rodent abundance, despite the wide range of observed population sizes, suggests that amounts of girdling are not a simple function of small rodent population densities.

Several studies have suggested that the consumption of large amounts of bark is indicative of food shortages, particularly a lack of carbohydrates (Hamilton 1941; Thompson 1965; Zemanek 1972; Hansson 1973a, 1973b). If this is true, then animals in areas with higher levels of damage should be in poorer condition than animals in areas with little or no damage. Levels of damage were significantly higher on the Tamarack study area, yet *C. gapperi* and *M. pennsylvanicus* populations on the Tamarack study areas were in moderate to good condition (based on population sizes, population trends, and reproduction; Section 3.6). Fat indices and condition indices of snap-trapped animals similarly indicated that *C. gapperi* and *M. pennsylvanicus* from tamarack habitats were in moderate to excellent nutritional condition. In contrast, the condition of *C. gapperi* in jack pine, aspen, black spruce, and open (treeless) habitats and of *M. pennsylvanicus* in jack pine and aspen communities tended to be below average--amounts of damage on these areas, however, were extremely low in both years of the study. The association between amounts of damage and nutritional condition of small rodents in this study suggest that bark consumption and poor nutritional condition are not as closely related as suggested in earlier studies. Studies of the seasonal changes in the nutritional condition of natural small rodent populations versus seasonal changes in nutrient availability are required to examine more closely the role of bark consumption in the nutritional status of free-ranging small rodents.

7.4.2 Damage by Snowshoe Hares

Wide variations in browsing pressure appear to be a common phenomenon associated with cyclic fluctuations in snowshoe hare populations. Pease et al. (1979) showed that over 50% of the woody stems ($\leq$1.5 cm in diameter) in natural forest communities of north-central Alberta had been severely browsed by snowshoe hares during a snowshoe hare population peak, whereas only 2% of the woody stems were so intensively browsed during the population decline and low. Keith and Windberg (1978) have suggested that the extreme reductions in the abundance and quality of forage associated with the more intensive browsing pressures of increasing snowshoe hare populations result in a decline in the nutritional condition of snowshoe hares. Changes in nutritional condition subsequently affect reproduction and eventually result in the initiation of the population decline. In addition, excessive clipping of trees and shrubs by snowshoe hares and other herbivores can severely curtail the growth of trees and shrubs and reduce the survival of these plants; moderate browsing, however, has been shown to simulate browse production (Garrison 1953; Stoeckler et al. 1957; Lay 1965; Krefting et al. 1966; Harlow and Halls 1972).

Snowshoe hares feed upon a wide variety of woody-stemmed plants during the late fall to early spring periods but show significant preferences and avoidances of some browse species. In the Athabasca Basin, *P. tremuloides*, *L. laricina*, and *P. banksiana* were the most highly preferred tree species and *B. glandulosa*, *Alnus* spp., *P. pensylvanica*, and *A. alnifolia* were the most highly preferred shrub species. Studies of snowshoe hare diets and feeding preferences in Newfoundland, Ontario, Alberta, and Alaska suggested that *P. tremuloides*, *Betula* spp., *Salix* spp., and *Alnus* spp. were the most commonly consumed or preferred forage species of snowshoe hares (Dodds 1960; de Vos 1964; Keith 1972; Klein 1977; Wolff 1978). *Picea* spp., *Pinus* spp., *L. laricina*, *Vaccinium* spp., *L. groenlandicum*, *Rosa* spp., *Corylus cornuta*, and *Viburnum* spp. also were preferred by snowshoe hares in some of these localities.

Of the tree and shrub species present in the Athabasca Basin, *B. papyrifera* was most resistant to browsing followed by *P. glauca*, *P. balsamifera*, and *P. mariana*. Shrubs such as *Lonicera* spp., *S. albus*, *S. canadensis*, *R. americanum*, *R. melanolasius*, and *Viburnum* spp. also sustained little or no browsing damage. Keith (1972), Klein (1977), and Pease et al. (1979) similarly noted that snowshoe hares in north-central Alberta and central Alaska rarely browsed shrubs of the family Caprifoliaceae (*Lonicera* spp., *S. albus*, *Viburnum* spp.). Klein (1977) suggested that limited browsing pressures on these species of shrubs and trees (particularly young suckers) are largely the result of antiherbivore chemistry (e.g., toxins, digestibility-reducing substances). Growth forms of shrubs and trees may also affect their susceptibility to damage (Klein 1977). Low woody-stemmed plants such as *S. canadensis*, *V. uliginosum*, and *L. groenlandicum* are all afforded some protection from hare browsing by the accumulated winter snows. Others, such as *Rosa* spp. or *Viburnum* spp., are protected partially from browsing by sharp spines or stiff remnants of the previous summer's inflorescence.

Because snowshoe hares preferentially browse some species of trees and shrubs, differences in amounts of damage among habitats may reflect the availability of these preferred species in some community types. Of the three most highly preferred species of trees, *P. tremuloides* and *P. banksiana* saplings were most abundant on the Aspen study area, whereas *L. laricina* was most abundant on the Tamarack and Black Spruce study areas (Tables 28 to 35); levels of browse damage to trees were also significantly higher on these three areas than on successional areas or in other natural forest communities. Of the four most highly preferred shrub species (*B. glandulosa*, *Alnus* spp., *P. pensylvanica*, and *A. alnifolia*), only *B. glandulosa* was more abundant on the study area (Tamarack study area) where amounts of browse damage to shrubs were significantly higher than in other areas. Overall, these associations between amounts of browse damage and the availability of preferred species of trees and shrubs suggest that feeding preferences do influence browsing activity and are partially associated with differences in the amount of damage among habitats.

Keith (1972) suggested that the density and composition of understory species are major habitat characteristics associated with snowshoe hare distributions and numbers and, consequently, the potential for browse damage. In this study, levels of damage were significantly correlated with both stem densities and several components of habitat structure. Overall, the tamarack understory and, to a lesser degree, the aspen understory and the absence of (i.e., a negative regression coefficient) balsam poplar understory were the most important habitat factors associated with higher levels of snowshoe hare damage.

The close associations of these habitat factors with amounts of damage suggest that both the availability of preferred browse species and cover were associated with browsing activity by snowshoe hares. High densities of *L. laricina* and *B. glandulosa* were major components of the tamarack understory; both were preferred browse species and would provide dense cover for snowshoe hares. Similarly, the high densities of *A. alnifolia* (preferred browse species) associated with aspen understory would provide an adequate supply of winter forage, whereas the dense growths of a number of unpalatable species (i.e., shrubs of the family Caprifoliaceae) would provide ample cover. By the same reasoning, the poor association between balsam poplar understory and damage appears contrary to the suggestion that food and cover are associated with the amount of damage; *Alnus* spp., a highly preferred browse species, were abundant in this area and the dense canopy typical of this community would provide ample cover. Most *Alnus* spp. on the Balsam Poplar study area, however, were large stems with little or no secondary branching below a height of 2 to 3 m. As a result, the more highly preferred parts of the plant [i.e., twigs and buds (Klein 1977)] would be inaccessible to snowshoe hares. Consequently, the availability of woody-stemmed forage during the winter may have been low on this area.

Snowshoe hare population sizes also may be a potentially important influence on amounts of damage within different habitats; amounts of browse in areas supporting higher numbers of hares would be expected to be higher than in areas with small population sizes. In this study, the significant and positive correlation between the amounts of new browse damage to shrubs and the numbers of snowshoe hares present during the previous winter suggest that some differences in the amounts of damage among habitats were the result of different population sizes. However, old damage to trees and shrubs did not appear to support this conclusion. Because old damage reflects browsing activity for several years prior to the sampling period, this poor association with population sizes is not unexpected. Keith and Surrendi (1971) and Keith and Windberg (1978) have suggested that habitat selection by snowshoe hares is influenced by cyclic changes in population density; snowshoe hares were restricted to areas of high quality habitat during population lows and only expanded into more marginal habitats as population densities increased. Consequently, browsing activity in different habitats also may be influenced by cyclic population changes (with the possible exception of high quality habitats) and amounts of browsing over a period of several years will not necessarily be related directly to the number of snowshoe hares present during one winter.

7.5 CONCLUSIONS

Overall, small rodent damage to most species of trees and shrubs in the Athabasca region was limited. Although levels of damage differed among habitat types in 1978 (trees and shrubs in tamarack habitats sustained the highest amounts of damage), these differences did not appear to be closely related to the population sizes of the three major small rodent species (*C. gapperi, M. pennsylvanicus,* and *P. maniculatus*), to nutritional condition, or to a number of habitat factors characterizing vegetation communities within the eight study areas. However, small rodents showed significant preferences for *P. tremuloides, B. papyrifera, B. glandulosa,* and *A. alnifolia.* Notably, *B. glandulosa* and *B. papyrifera* were abundant on the Tamarack study area, relative to the other study sites, suggesting that inter-habitat differences in levels of damage may reflect differences in the availability of more highly preferred species in different habitats.

Browsing damage by snowshoe hares was observed more commonly in the AOSERP study area than was girdling damage by small rodents; this probably reflects the reliance on woody-stemmed plants by snowshoe hares for much of their winter diet. Of the naturally occurring species of trees and shrubs in the region, *P. tremuloides, L. laricina* and *P. banksiana* were the most susceptible tree species and *B. glandulosa, Alnus* spp., *P. pensylvanica,* and *A. alnifolia* were the most susceptible shrub species to snowshoe hare damage. In contrast, *B. papyrifera, P. glauca, P. mariana, P. balsamifera, R. americanum, R. melanolasius, Rosa* spp., and members of the family Caprifoliacea rarely were damaged by snowshoe hares. Differences in the amounts of damage by snowshoe hares to trees and shrubs in each study area suggested that both food availability (i.e., the presence of high densities of preferred tree and shrub species) and the density of tree and shrub cover were strongly associated with levels of browse damage.

8. CONCLUSIONS

The broad objectives of AOSERP as described by Smith (1979) were to develop a comprehensive environmental research program which would (1) establish an integrated data base for future environmental management strategies and (2) identify environmental and social problems that can be expected to arise from present and proposed oil sands developments. The Land System research program, of which this study is a part, has concentrated primarily on documentation of the physiographic and biophysiographic features of the AOSERP study area, as well as describing the major faunal groups and their habitat affinities. This research program has attempted to specifically identify population sizes and distributions of small mammals in natural and successional plant communities, and to evaluate the importance (i.e., quality) of the major habitat types for each of the major species. By identifying the habitat affinities of each species, impacts of habitat loss resulting from oil sands developments can be better described and mitigative measures can be planned more effectively. Consideration of such data may involve direct effects on small rodents or indirect effects on other components of the ecosystem such as predators or vegetation. An additional objective of this study was to determine the extent and nature of small mammal damage to trees and shrubs in natural habitats. Information obtained was intended primarily for comparison with concurrent studies of small mammal damage to woody-stemmed plants in existing reclamation areas in the Athabasca Basin.

Conclusions presented here are intended primarily to provide an overview of small mammal populations in the AOSERP study area and of the importance and use of habitats by small mammals. Possible impacts on these species from habitat loss resulting from oil sands developments are also considered.

8.1 SMALL MAMMAL POPULATIONS

In terms of population sizes and distributions, four species of small mammals, *C. gapperi*, *M. pennsylvanicus*, *P. maniculatus*, and *L. americanus*, were important components of the boreal forest ecosystem in the AOSERP study area. Although a number of other small mammals, including *Microsorex hoyi, Sorex cinereus, Sorex obscurus, Sorex arcticus, Phenacomys intermedius, Synaptomys borealis, Zapus hudsonicus, Eutamias minimus, Tamiasciurus hudsonicus, Glaucomys sabrinus, Mustela nivalis,* and *Mustela erminea,* were captured, numbers were insufficient for further analysis. This does not imply, however, that these species are not important components of the boreal forest ecosystem. Such low abundances may reflect both small actual population sizes and/or biases in the sampling methods of this study (i.e., trapping methods used were specifically for small rodents and snowshoe hares).

8.1.1 *Clethrionomys gapperi*

Based on six different indices of habitat quality, balsam poplar, aspen, and jack pine communities were consistently the highest quality habitats for *C. gapperi*. Successional areas, black spruce forests, and tamarack forests were moderately suitable habitats for this species. In contrast, willow shrub cover was the lowest quality habitat of the communities studied.

Although numbers of *C. gapperi* varied greatly among major forest cover types, animals were consistently present in all communities, suggesting that all forest communities were suitable for this species (Douglass 1976a). Indices of reproductive success and dispersal, however, indicated that productivity and stability of *C. gapperi* populations varied among habitats. Dispersal indices suggested that populations in aspen, jack pine, balsam poplar, and black spruce habitats were composed primarily of resident animals; survival rates were high, recruitment by natality was high, and emigration was limited. In contrast, animals in willow and successional communities were largely transients; survival on these areas tended to be low, recruitment was predominantly by immigration, and emigration was high. Tamarack forests supported moderate numbers of resident animals but emigration and immigration were also high.

Reproductive success appeared to be directly associated with the 'stability' of animals in these habitats; reproductive success tended to be higher in populations with higher numbers of resident animals, as opposed to those with higher numbers of transients. This may be indicative of the suitability of areas for breeding and survival (e.g., food supplies, protective cover, moisture, numbers of predators) but may also reflect the types of animals present in these areas. Studies of dispersal of small rodents (Myers and Krebs 1971; Krebs et al. 1976) have suggested that dispersing animals (i.e., immigrants to less suitable habitats) are genetically, reproductively, and behaviourally different from resident animals.

Habitat selection by small mammals is a complex response of a species to a number of biotic and abiotic components which in turn determine the quality of an area for that species. The determination of the factors important to each species (i.e., the determinants of a species' niche) has been the subject of a number of recent and detailed research programs (e.g., Rosenweig 1973; M'Closkey 1976; Deuser and Shugart 1978, 1979). Although it was not possible to identify factors directly influencing habitat selection by *C. gapperi* in this study, several habitat components, associated with food resources and protective cover, appeared to be closely related to habitat use by this species.

Associations of higher numbers of *C. gapperi* with dense shrub understories composed of *C. stolonifera*, *Ribes* spp., *Alnus* spp., and/or *R. melanolasius*; dense ground cover; and moderate to thick accumulations of litter and deadfall mean that plants or conditions associated with these habitat factors are of importance in determining the level of use of areas by *C. gapperi*. *Clethrionomys gapperi* also preferred areas of tree cover dominated by *P. balsamifera* or *L. laricina* and shrub cover dominated by *Rosa* spp., *Viburnum* spp., *Alnus* spp., or *B. glandulosa*. Preferences may again indicate a direct relationship between these tree and shrub species and the abundance of *C. gapperi* but may also reflect a relationship with other biophysical factors that are associated with these plant species.

Dietary analyses suggest that the direct association of *C. gapperi* with these plant species is not a result of feeding habits. None of the above-mentioned tree, shrub, or ground cover species were important dietary items--during 1979, lichens, mycorrhiza, arthropods, *Salix* spp., *Equisetum* spp., and mushrooms were the primary foods of *C. gapperi*. Although quantitative information on the availability of these major food items in each habitat was not available, studies by Stringer (1976) and Maser et al. (1979) suggest that lichens and mycorrhiza, respectively, are generally more abundant in mature forested areas. Dense ground cover and thick accumulations of litter and deadfall also are associated with higher numbers of arthropods (Ryan and Hilchie 1980). The association of *C. gapperi* with aspects of habitat structure, that are also related to a higher availability of important foods, suggests that forage availability does influence habitat selection by this microtine. Further studies of this aspect of habitat selection by *C. gapperi* are required.

The significant avoidance of areas with no shrub cover, and the association of high numbers of *C. gapperi* with higher densities of some shrub species, also suggests that dense shrub cover is an important aspect of habitat structure for *C. gapperi*. Dense shrub cover may afford protection from climatic extremes and some predators while providing a suitable microclimate (e.g., moisture, temperature) for *C. gapperi* and for its major dietary components.

Habitat associations discussed here were representative of the late spring to late fall period. Studies of a closely-related species, *Clethrionomys rutilus*, by West (1977) indicated that small rodent habitat affinities can change drastically between seasons, particularly during the winter in more temperate regions. Because *C. gapperi* populations may exhibit similar seasonal shifts in habitat use, the habitat affinities described here should not be applied to winter and early spring.

8.1.2 *Microtus pennsylvanicus*

Indices of habitat quality consistently ranked willow and successional communities as the highest quality habitats for

M. pennsylvanicus. Tamarack and black spruce forests were moderately suitable for this vole, whereas aspen, jack pine, and balsam poplar were most poorly suited.

Douglass (1976a) suggested that population sizes as well as the consistency of occurrence of animals were important indices of habitat quality. Peak population densities of *M. pennsylvanicus* differed greatly among study areas in this study but, with the exception of jack pine forests, all habitats studied appeared capable of continually supporting at least moderate numbers of this vole. Numbers of mice on the Jack Pine study area in 1979, however, were low and highly variable.

As discussed for *C. gapperi*, dispersal indices offer another means of evaluating the 'stability' of animals in populations. Dispersal indices of *M. pennsylvanicus* in jack pine, balsam poplar, older successional, and black spruce cover types suggested that populations in these areas were composed predominantly of transient animals (i.e., high rates of immigration). In contrast, dispersal indices in aspen, willow, young successional, and tamarack communities suggested that most animals present were residents (i.e., high recruitment by natality, little emigration). The latter four habitat types therefore would appear to be the most stable habitats for this vole.

If reproductive success is related to habitat selection (Krebs 1978), reproductive success of predominantly resident populations in high quality habitats would be expected to be greater than that of transient populations in poor quality habitats. Close associations of reproductive success with the 'stability' of *M. pennsylvanicus* populations, however, were not apparent. High numbers of resident animals only were associated with high reproductive success in young successional areas in 1978 and in successional areas and tamarack forests in 1979. Poor reproductive success only was associated with higher numbers of transient animals in balsam poplar and older successional areas in 1978 and in jack pine and balsam poplar forests in 1979. However, during the peak and decline phases of a microtine population cycle, reproduction of dispersing animals has been found to be higher than non-dispersing animals (i.e., more young female animals were in breeding condition) (Myers and Krebs 1971). Because *M. pennsylvanicus* populations in the AOSERP study area were in the peak and decline phase of the cycle during this study, disproportionate dispersal of young breeding animals from optimal habitats to more marginal habitats may have resulted in the poor associations between reproductive success and dispersal indices in this study.

Assuming that willow and successional habitats are the best quality habitats for *M. pennsylvanicus* in the Athabasca Basin, a number of vegetation characteristics appeared related to these high evaluations of habitat quality. The preference of *M. pennsylvanicus* for successional areas or grass meadows (i.e., no trees or shrubs) and the significant association of *M. pennsylvanicus* with habitat factors characterizing dense successional cover and grass/sedge cover suggest that dense graminoid or forb cover and sparse tree or shrub cover provide near-optimal conditions for this species. Graminoids and mycorrhiza were the predominant foods of *M. pennsylvanicus* in this study although arthropods, *Salix* spp., moss, and *Equisetum* spp. were present seasonally in small amounts. Assuming that arthropods are also moderately abundant in successional areas and willow shrub communities (Ryan and Hilchie 1980), the best quality habitats appear to offer high availabilities of the most common foods of this vole. In addition, the dense graminoid or forb cover in these areas would afford protection from climatic extremes and aerial predators.

Based on existing information, it is not possible to determine whether food availabilities or cover factors are most important. However, a recent study by Green (1980), in which food supplies and cover were manipulated on experimental reclamation areas, suggests that the plant cover is more important than food supplies--*M. pennsylvanicus* was very abundant in an area with dense grass/legume cover and supplemental food but was limited in an area with supplemental food and highly reduced ground cover.

Habitat affinities of *M. pennsylvanicus* in this study were generally the converse of those of *C. gapperi*. Although a number of factors related to vegetation structure likely influenced the habitat affinities of each species, differences in habitat use suggest that spatial segregation of *C. gapperi* and *M. pennsylvanicus* is also an important aspect of habitat use. Studies of interspecific competition between these species (Grant 1969, 1970, 1972; Morris 1969; Morris and Grant 1972) clearly indicate that each species in its preferred habitat is able to restrict the distribution of the other. Ideally, interspecific competition should have been included in evaluations of habitat use in this study (e.g., as a component of habitats in the SMR analyses); however, because of time and budgetary constraints, analyses of interspecific competition were not possible.

8.1.3 *Peromyscus maniculatus*

Balsam poplar and young successional areas were the highest quality habitats for *P. maniculatus* in the AOSERP study area; almost all indices of habitat quality in these communities were high. Aspen and jack pine forests were moderately suitable for *P. maniculatus*, whereas older successional, black spruce, willow, and tamarack communities were only marginally suitable.

Both willow shrub and tamarack forest appeared uninhabitable for *P. maniculatus*; no *P. maniculatus* were captured on live-trapping areas in these habitats. Based on peak MNAs and consistency of occurrence (Douglass 1976a), jack pine and black spruce also were not consistently suitable habitats for this species. All other habitats, however, consistently supported some *P. maniculatus* throughout the trapping season in each year, suggesting that these communities were stable habitats for this cricetid.

Indices of dispersal and reproductive success similarly suggested that aspen, balsam poplar, and young successional areas were more stable communities for *P. maniculatus*; most animals present in these areas were residents and reproductive success was high. In contrast, most animals in black spruce habitat were transients and reproductive success was low. Older successional communities generally were composed of both residents and transients and reproductive success was moderate to low. Black spruce communities, in particular, may serve as 'dispersal sinks' for dispersing, non-breeding young animals where competition for food resources and nest sites are less intense (Fairbairn 1978).

Multivariate associations of habitat structure with numbers of *P. maniculatus* and preferences for specific habitats suggested that *P. maniculatus* were habitat generalists and were not strongly associated with any one habitat. Dense shrub understories, deadfall, and moderate accumulations of litter, however, were generally associated with higher numbers of this species and *A. balsamifera, P. balsamifera,* and *Alnus* spp. were significantly preferred by *P. maniculatus*.

The availability of arthropods, the most common food of *P. maniculatus* in the Athabasca region, did not appear related to habitat use. Poor quality habitats for *P. maniculatus*, such as fens, non-vegetated areas, and lightly forested tamarack bogs, had the highest arthropod standing crop (biomass$\cdot$m^2), whereas higher quality habitats, such as balsam poplar (= mixed woods), aspen, and jack pine forest, had some of the lowest standing crop estimates (Ryan and Hilchie 1980). However, *P. maniculatus* may prefer some species of arthropods which actually may be more abundant in these latter habitats.

The observed habitat associations for *P. maniculatus* may also reflect selection of more suitable microclimates, availabilities of nest sites, better protection from predators, and/or the influence of interspecific competition as previously described. For example, interspecific competition between *P. maniculatus* and *M. pennsylvanicus*, as described by Grant (1971b), may have resulted in the restriction of *P. maniculatus* distributions by *M. pennsylvanicus*, particularly during 1978 when *M. pennsylvanicus* populations were at a peak.

8.1.4 *Lepus americanus*

Snowshoe hares were most abundant in black spruce forests and were most strongly associated with vegetation factors characterizing black spruce communities. Balsam poplar forests appeared to be moderately suitable, whereas aspen and jack pine forests were only marginally suitable for snowshoe hares. Because of budgetary constraints, snowshoe hare populations in other major vegetation types could not be sampled. Estimates of snowshoe hare browse, however, suggested that tamarack forest was also an important habitat for snowshoe hares, whereas successional areas were only marginal habitats for this species.

Distributions of snowshoe hares were most strongly associated with *L. laricina* and *P. mariana* tree cover and *Salix* spp. shrub cover. Ground cover, dominated by moss, *L. groenlandicum*, and *V. vitis-idaea*, was also associated with higher numbers of snowshoe hares. Estimates of snowshoe hare browse in each habitat type indicated that *L. laricina* as well as *P. tremuloides* and *P. banksiana* were the most preferred tree species. *Betula glandulosa, Alnus* spp., *P. pensylvanica,* and *A. alnifolia* were the most highly preferred species of shrubs. In contrast, *P. mariana* (the other tree species associated with high numbers of snowshoe hares), as well as *P. glauca, P. balsamifera, B. papyrifera, R. americanum, R. melanolasius, Rosa* spp., and members of the family Caprifoliaceae were not commonly eaten by snowshoe hares. Associations of *L. americanus* in this study with both preferred and less common browse species support the suggestion by Keith (1972) that dense forest cover as well as food availability are important factors in the selection of habitats by snowshoe hares.

8.2 IMPACTS OF OIL SANDS DEVELOPMENTS

Habitat loss associated with the development of oil sands facilities will most likely be the major impact of such developments for small mammals. However, because of the wide distribution of small mammals in northeastern Alberta in relation to the small amounts of land disturbances now anticipated as a result of current and planned oil sands developments, impacts on small mammals will be limited. Current information on more complex questions, such as the effect of aerial emissions on vegetation or the bioaccumulation of heavy metals, is too limited to permit evaluations of impacts arising from these aspects of oil sands developments.

Based on indices of habitat use and quality discussed in this study, it is apparent that wide-scale changes in habitat structure or disproportionate losses of some habitats could result in significant changes in small mammal populations. In turn, changes in the species composition or abundance of small mammals may affect mammalian and avian predators, soil dynamics and development, vegetation productivity and composition, and insect numbers (see Section 1).

Of the natural habitats studied, balsam poplar communities were the most important small mammal habitat; use of this community by *C. gapperi*, *P. maniculatus*, and *L. americanus* was high. Loss of balsam poplar communities would most seriously affect *C. gapperi* populations. Numbers and productivity of this species was higher in balsam poplar forest than in any other habitat. *Lepus americanus* and *P. maniculatus* would likely be affected to a lesser extent; *L. americanus* more commonly used black spruce habitats, whereas *P. maniculatus*, a habitat generalist, was abundant in several other habitats.

Black spruce and tamarack forests were the least important small rodent habitats but were the highest quality snowshoe hare habitats. Numbers and productivity of snowshoe hares in black spruce communities were high and estimates of snowshoe hare browse in tamarack communities suggested that this habitat was an important feeding area, if not an important breeding and overwintering site.

Jack pine and aspen communities appeared to be moderately suitable habitats for most small mammals, except *M. pennsylvanicus*. Loss of these habitats consequently would have a minimal effect on the major small mammal species. The diversity of small mammals in aspen habitats, however, was higher than in any other community sampled; in particular, many of the less common species occurred in this forest type.

Successional communities were intensively used by both *P. maniculatus* and *M. pennsylvanicus*. The suitability of these areas, however, was dependent on the age of the community. Use of an older (5 year old) successional area by *P. maniculatus* was limited suggesting that only young successional communities are suitable habitats for this species. If one assumes that willow shrub habitats are also seral habitats, representing a later stage of the successional continuum, snowshoe hare use of successional habitats also appears time dependent. Based on amounts of browse, snowshoe hares avoided younger successional areas but had begun to commonly utilize willow shrub communities. Willow shrub communities were also commonly used by *M. pennsylvanicus* but were totally avoided by *P. maniculatus*.

Clearing of forest cover, consequently, will both detrimentally and beneficially affect small mammals. Loss of mature forested communities will most seriously affect *C. gapperi* and *L. americanus* populations and will moderately affect *P. maniculatus* populations. The long regeneration time of these communities in reclamation sites, if in fact they will be regenerated, will prolong these adverse effects. In particular, black spruce and tamarack communities typical of poorly drained areas will likely not be reclaimable on the well-drained sand deposits typical of reclamation sites. Loss of these habitats, the highest quality habitats for snowshoe hares, consequently, will be permanent. Unless such losses of mature forest communities are widespread, however, it is unlikely that effects on small rodents or snowshoe hares will even be detectable.

In contrast, assuming that natural successional processes are allowed to proceed in some areas, land disturbances may actually benefit *M. pennsylvanicus*. *Peromyscus maniculatus* may also initially benefit from the increased seral growth. Similarly, the creation of reclamation areas dominated by dense growths of graminoids and legumes may also benefit these two small rodent species. This assumes, however, that sources of 'surplus' (dispersing) animals are present in adjacent habitats. If succession in disturbed but naturally revegetating areas or in reclamation sites proceeds to dense growths of *Salix* spp. and perhaps young aspen forests, snowshoe hares may also eventually benefit from oil sands related disturbances (Keith 1972; this study).

9. RECOMMENDATIONS

9.1 FURTHER STUDIES

As a result of time and budgetary constraints, the proposed 4 year study of small mammal populations in natural communities of the AOSERP study area was terminated following the second year of study. In view of the limitations of this study in relation to cyclic population phenomenon of small mammals, some of the proposed objectives of this study could not be fulfilled. To complete a detailed baseline study of small mammals in the AOSERP study area, further information is currently required on:

1. Variation in population characteristics of the major species of small mammals in each of the major habitats throughout a complete population cycle (i.e., a minimum of a 4 year period) and the relationship of these characteristics to habitat quality;
2. Responses of small mammals to specific components of vegetation structure throughout a full population cycle;
3. The role of interspecific competition in habitat selection by small mammals;
4. The composition of diets throughout the year (in particular, information on winter and early spring diets is required); the relationships between feeding habits, the availability of preferred or commonly consumed foods, and habitat selection; and the nature and importance of bark tissue of trees and shrubs in small rodent diets; and
5. The extent of small mammal damage, particularly small rodent damage, throughout a complete population cycle and the relationships between the condition of small rodents, nutrient availability, and amounts of girdling.

Because of the importance of small mammals as herbivores of the boreal forest ecosystem, and the likelihood of increased aerial emissions of gaseous and particulate toxic compounds with increased oil sands developments, it is also important that the role of small rodents in the transfer of such compounds from vegetation to higher trophic levels (i.e., predators) be established and the potential for bioaccumulation of these substances by small mammals be defined. Physiological and demographic implications of these substances on small mammals should also be explored.

9.2 MITIGATION OF IMPACTS OF OIL SANDS DEVELOPMENTS

Based on present knowledge, the potentially most serious impact of oil sands developments on small mammals will be the loss of habitat associated with site development, mining, tailings ponds, townsites, and access routes. Of the major forest types in the AOSERP study area, balsam poplar forests were the most important habitat for small rodents, whereas black spruce and, possibly, tamarack forests were the most important habitats for snowshoe hares. On the other hand, jack pine and aspen forests were less important habitats for small mammals.

Because the amounts of land disturbed by oil sands developments are anticipated to be small (in relation to the availability of the major forest cover types in the Athabasca Basin), impacts of habitat loss on small mammals is not expected to be severe. However, disturbances of jack pine and, possibly, aspen forests in lieu of disturbances of balsam poplar, black spruce, or tamarack communities would help to minimize adverse effects on populations of the major small mammal species. In addition, because the regrowth of mature forest communities (on which *C. gapperi* and *L. americanus* are dependent) on reclamation sites will be slow, if feasible, it is recommended that some enclaves of mature forest communities be maintained adjacent to reclamation sites.

Current reclamation practices employed in the Athabasca Oil Sands result primarily in dense growths of agronomic grasses and legumes and sparse tree or shrub cover. Establishment of native successional species appears slow (Green 1980). Impacts of mining disturbances on small mammals may be mitigated by reclamation programs that mimic natural successional processes. Such practices would likely benefit *M. pennsylvanicus* and *P. maniculatus* and if capable of proceeding to later seral stages (i.e., dense shrub growths, young aspen forests), may also moderately benefit snowshoe hares. However, because the current design of most reclamation sites and tailings dikes result in deep deposits of well-drained sandy soils, mining disturbances will result in a net loss of vegetation communities typical of wet sites. It is recommended that some reclamation practices also attempt to re-establish communities typical of poorly-drained sites, such as black spruce or tamarack bogs. Such practices would primarily benefit the snowshoe hare component of the small mammal community.

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11. APPENDICES

Appendices have been organized to correspond to sections in the main text.

11.1 PLANT NOMENCLATURE (Table 41)

Table 41. Scientific and common names of plant species encountered during vegetation surveys in 1978 and 1979. [Scientific and common names from Moss (1967) unless otherwise indicated.]

Scientific Name	Common Name
Abies balsamea	balsam fir
Acer glabrum	Manitoba maple
Achillea millefolium	common yarrow
Achillea sibirica	many-flowered yarrow[a]
Actaea rubra	baneberry
Alnus spp.	alder
Amelanchier alnifolia	saskatoon
Anaphalis margaritacea	pearly everlasting
Andromeda polifolia	bog rosemary
Anemone multifida	cut-leaved anemone
Apocynum androsaemifolium	spreading dogbane
Aquilegia brevistyla	blue columbine
Aralia nudicaulis	wild sarsaparilla
Arctostaphylos rubra	alpine bearberry
Arctostaphylos uva-ursi	bearberry
Arenaria spp.	sandwort
Aster spp.	aster
Aster conspicuus	showy aster
Aster puniceus	purple-stemmed aster
Betula glandulosa	dwarf birch
Betula occidentalis	water birch
Betula papyrifera	paper birch
Betula pumila	swamp birch
Caltha palustris	marsh marigold
Chamaedaphne calyculata	leather-leaf
Chenopodium album	lamb's-quarters

continued...

Table 41. Continued.

Scientific Name	Common Name
Chenopodium capitatum	strawberry blite
Cicuta spp.	water hemlock
Circaea alpina	enchanter's nightshade
Cladina/Cladonia spp.	reindeer moss
Clematis verticellaris	purple clematis
Commandra pallida	bastard toad-flax
Cornus canadensis	bunchberry
Cornus stolonifera	red osier (dogwood)
Corydalis aurea	golden corydalis
Corydalis sempervirens	pink corydalis
Crepis tectorum	annual hawksbeard
Cypripedium spp.	lady's-slipper (moccasin-flower)
Delphinium glaucum	tall larkspur
Empetrum nigrum	crowberry
Epilobium angustifolium	fireweed
Equisetum spp.	horsetail
Equisetum sylvaticum	woodland horsetail
Fragaria virginiana	wild strawberry
Galeopsis tetrahait	hemp nettle
Galium boreale	northern bedstraw
Galium triflorum	sweet-scented bedstraw
Geranium bicknellii	Bicknell's geranium[a]
Geum rivale	purple or water avens
Geum triflorum	old man's whiskers
Habenaria hyperborea	northern green orchid
Hackelia spp.	stick-seed
Hieracium canadense	Canada hawkweek
Hieracium umbellatum	narrow-leaved hawkweed

continued...

Table 41. Continued.

Scientific Name	Common Name
Impatiens spp.	jewelweed
Kalmia polifolia	mountain laurel
Labiatae spp.	mint
Larix laricina	tamarack
Lathyrus ochroleucus	vetchling
Ledum glandulosum	glandular labrador tea
Ledum groenlandicum	common labrador tea
Lilium philadelphicum	western wood lily
Linnea borealis	twin-flower
Lonicera spp.	honeysuckle
Lycopodium complanatum	ground cedar
Maianthemum canadense	wild lily-of-the-valley
Matricaria matricarioides	pineapple-weed
Medicago sativa	alfalfa
Melilotus alba/officinalis	sweet clover
Menyanthes trifoliata	buck-bean
Mertensia paniculata	tall mertensia
Mitella nuda	bishop's-cap
Oplopanax horridum	devil's-club
Orchis rotundifolia	round-leaved orchid
Oxycoccus microcarpus	small bog cranberry
Parnassia spp.	grass-of-parnassus
Pedicularis spp.	lousewort
Petasites spp.	sweet coltsfoot
Petasites palmatus	palmate-leaved coltsfoot
Petasites sagittatus	arrow-leaved coltsfoot
Picea glauca	white spruce
Picea mariana	black spruce

continued...

Table 41. Continued.

Scientific Name	Common Name
Pinus banksiana	Jack pine
Plantago major	plantain
Polypodiaceae spp.	ferns
Populus balsamifera	balsam poplar
Populus tremuloides	aspen
Potentilla spp.	cinquefoil
Potentilla concinna	early cinquefoil
Potentilla fruticosa	shrubby cinquefoil
Potentilla palustris	marsh cinquefoil
Potentilla rivalis	brook cinquefoil[a]
Potentilla tridentata	three-toothed cinquefoil
Prunus pensylvanica	pin cherry
Prunus virginiana	chokecherry
Pyrola asarifolia	common pink wintergreen
Pyrola secunda	one-sided wintergreen
Ranunculus spp.	buttercup
Rosa acicularis	prickly rose
Rosa woodsii	woodland rose
Ribes americanum	wild black currant
Ribes oxyacanthoides/hirtellum	wild gooseberry
Ribes triste	wild red currant
Rubus acaulis	dwarf raspberry
Rubus chamaemorus	cloudberry
Rubus melanolasius	wild red raspberry
Rubus pubescens	dewberry
Salix spp.	willow
Salix bebbiana	beaked willow
Scirpus spp.	bulrush

continued...

Table 41. Concluded.

Scientific Name	Common Name
Senecio lugens	ragwort
Shepherdia canadensis	Canadian buffalo-berry
Sium suave	water parsnip
Smilacina racemosa	false solomon's-seal
Smilacina stellata	star-flowered solomon's-seal
Solidago	goldenrod
Stellaria spp.	chickweed
Stellaria longifolia	long-leaved chickweed
Streptopus amplexifolius	twisted-stalk
Symphoricarpos albus/occidentalis	snowberry
Taraxacum spp.	dandelion
Trientalis europaea	star-flower
Trifolium pratense	red clover
Typha latifolia	common cattail
Urtica gracilis	common nettle
Vaccinium caespitosum	dwarf bilberry
Vaccinium myrtilloides	blueberry
Vaccinium uliginosum	bog bilberry
Vaccinium vitis-idaea	bog cranberry
Viburnum edule	low-bush cranberry
Viburnum trilobum	high-bush cranberry
Vicia americana	wild vetch
Viola spp.	violet
Viola adunca	early blue violet
Viola palustris	marsh violet
Viola renifolia	kidney-leaved violet
Viola rugulosa	Western Canada violet

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[a] Common name from Looman and Best (1979).

11.2 SMALL RODENT DEMOGRAPHY (Tables 42 to 49)

Table 42. Captures of other species of small mammals during snap-trap censuses in 1978 and 1979.

Date	Total Number of Trap-nights[a]	Captures per Trap-night					
		S. cinereus/ *M. hoyi*[b]	*S. obscurus*/ *S. arcticus*[c]	*S. borealis*	*P. intermedius*	*Z. hudsonicus*	*E. minimus*
1978							
July	1748	0.11 ± 0.13	0.0	0.0	0.0	0.11 ± 0.07	0.51 ± 0.23
August	3231	1.80 ± 0.38	0.0	0.0	0.03 ± 0.03	0.15 ± 0.07	0.03 ± 0.04
October	1205	2.24 ± 0.65	0.0	0.0	0.0	0.0	0.0
1979							
May	1079	0.09 ± 0.09	0.0	0.0	0.0	0.0	0.19 ± 0.16
June	1263	0.0	0.0	0.0	0.0	0.32 ± 0.12	0.0
July	1322	0.08 ± 0.07	0.0	0.08 ± 0.07	0.0	0.0	0.15 ± 0.15
August	1823	0.44 ± 0.37	0.11 ± 0.08	0.0	0.0	0.16 ± 0.09	0.0
September	1150	0.96 ± 0.46	0.09 ± 0.08	0.09 ± 0.09	0.0	0.17 ± 0.12	0.17 ± 0.13
October	1333	0.0	0.0	0.0	0.08 ± 0.07	0.0	0.0
November	1261	0.0	0.08 0.08	0.08 ± 0.09	0.0	0.0	0.0

[a] Total number of possible trap-nights minus trap setoffs.

[b] *M. hoyi* and *S. cinereus* could not be reliably differentiated on the basis of external characteristics and have consequently been grouped together.

[c] *S. obscurus* and *S. arcticus* could not be reliably differentiated on the basis of external characteristics and have consequently been grouped together.

Table 43. Breeding activity of mature *C. gapperi*. (Numbers of mature males and females captured and proportion in breeding condition during each trapping period are indicated for the summer periods of 1978 and 1979.)

	Aspen				Jack pine				Willow				Balsam poplar			
	Males		Females		Males		Females		Males		Females		Males		Females	
Date^a	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978																
1 July	1.00	4	1.00	2	0.50	2	1.00	3	-	0	-	0	0.75	4	1.00	6
19 July	0.67	3	1.00	2	-	0	1.00	2	-	0	1.00	1	0.58	12	0.67	9
1 August	1.00	2	1.00	2	0.67	3	1.00	3	-	0	-	0	0.47	15	0.50	12
16 August	0.33	3	1.00	3	-	0	1.00	1	0.50	2	0.50	2	0.33	15	0.23	13
27 August	0.00	3	0.80	5	0.33	3	-	0	0.00	2	0.00	1	0.11	9	0.33	12
15 September	0.00	9	0.56	9	0.20	5	0.25	4	0.00	9	0.00	3	0.05	19	0.38	13
1979																
16 May	1.00	12	1.00	6	1.00	7	0.83	6	1.00	3	1.00	1	0.90	10	0.80	5
8 June	1.00	11	0.50	6	1.00	5	0.80	5	1.00	2	-	0	1.00	6	1.00	3
24 June	1.00	11	0.63	8	1.00	3	1.00	5	1.00	2	-	0	1.00	6	0.75	4
18 July	0.80	15	0.85	13	0.75	8	0.75	8	0.75	4	0.50	2	1.00	5	0.86	7
10 August	0.40	15	0.54	13	0.67	9	0.63	8	0.50	4	0.50	2	0.29	17	0.50	14
31 August	0.53	17	0.20	20	0.38	13	0.38	8	0.00	4	0.50	2	0.06	18	0.21	24
20 September	0.14	14	0.09	22	0.08	12	0.17	6	0.00	8	0.20	10	0.10	21	0.11	19

continued...

Table 43. Concluded.

	Poplar Creek				Black spruce				Thickwood				Tamarack			
	Males		Females		Males		Females		Males		Females		Males		Females	
Date[a]	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978																
1 July	-	0	-	0	1.00	3	-	0	-	0	-	0	-	0	-	0
19 July	-	0	-	0	1.00	2	1.00	3	0.00	3	1.00	1	0.67	3	1.00	1
1 August	0.33	3	0.50	8	0.67	6	1.00	1	0.00	4	0.50	2	0.20	5	0.80	5
16 August	0.00	11	0.10	10	0.20	5	0.25	4	0.25	4	1.00	3	0.33	3	0.00	2
27 August	0.00	2	0.13	8	0.11	9	0.40	5	0.00	2	0.75	4	0.17	6	0.14	7
15 September	0.00	11	0.15	13	0.00	8	0.00	5	0.00	5	-	0	0.00	12	0.00	9
1979																
16 May	0.80	5	1.00	5	1.00	11	1.00	7	0.75	4	0.71	7	1.00	21	0.79	14
8 June	1.00	2	1.00	3	1.00	8	0.67	6	1.00	2	1.00	2	1.00	13	0.88	8
24 June	1.00	4	1.00	4	0.86	7	0.86	7	1.00	2	0.67	3	1.00	8	0.86	7
18 July	1.00	2	0.00	1	0.60	10	0.67	6	1.00	4	0.80	5	0.88	8	0.80	5
10 August	1.00	1	1.00	1	0.33	6	0.38	8	1.00	1	0.75	8	0.50	8	0.40	5
31 August	0.33	3	0.67	3	0.40	5	0.13	8	0.33	3	0.29	7	0.36	11	0.33	9
20 September	0.20	5	0.50	4	0.13	8	0.00	5	0.50	2	0.33	6	0.22	18	0.00	8

[a] Date shown is mid-point of trapping period.

Table 44. Breeding activity of mature *M. pennsylvanicus*. (Numbers of mature males and females captured and proportion in breeding condition during each trapping period are indicated for the summer periods of 1978 and 1979.)

	Aspen				Jack pine				Willow				Balsam poplar			
	Males		Females		Males		Females		Males		Females		Males		Females	
Date[a]	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978																
1 July	-	0	-	0	0.50	2	0.00	1	1.00	6	0.33	3	1.00	3	-	0
19 July	1.00	2	-	0	-	0	-	0	0.00	3	-	0	0.67	3	1.00	2
1 August	-	0	0.00	1	1.00	1	1.00	1	0.20	5	0.67	3	-	0	1.00	1
16 August	1.00	1	-	0	-	0	0.67	3	0.50	4	0.67	3	1.00	1	1.00	1
27 August	0.50	2	0.00	2	0.00	1	1.00	1	0.00	4	0.43	7	0.00	1	1.00	1
15 September	-	0	-	0	0.00	1	-	0	0.00	5	0.00	7	1.00	1	-	0
1979																
16 May	1.00	2	1.00	1	-	0	-	0	1.00	5	0.50	2	0.67	3	0.00	2
8 June	1.00	2	-	0	-	0	-	0	1.00	2	-	0	-	0	-	0
24 June	1.00	1	1.00	1	1.00	1	-	0	1.00	4	1.00	1	0.67	3	-	0
18 July	1.00	4	1.00	2	1.00	1	-	0	1.00	9	0.50	8	1.00	2	0.75	4
10 August	-	0	-	0	-	0	-	0	0.70	10	0.57	7	1.00	3	0.57	7
31 August	-	0	1.00	1	-	0	-	0	0.71	7	0.13	8	0.67	3	0.67	6
20 September	-	0	0.00	1	-	0	-	0	0.33	9	0.25	4	0.67	3	0.14	7

continued...

Table 44. Concluded.

Date[a]	Poplar Creek				Black spruce				Thickwood				Tamarack			
	Males		Females		Males		Females		Males		Females		Males		Females	
	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978																
1 July	-	0	-	0	1.00	4	-	0	1.00	1	-	0	1.00	1	-	0
19 July	-	0	-	0	0.67	3	1.00	2	1.00	2	1.00	5	1.00	5	0.60	5
1 August	0.18	11	0.83	6	0.67	6	1.00	7	1.00	2	1.00	6	0.25	4	1.00	2
16 August	0.25	4	0.63	11	0.33	9	0.83	6	0.50	4	1.00	7	0.44	9	0.50	8
27 August	0.25	8	0.43	14	0.17	12	0.20	5	0.43	7	0.78	9	0.00	9	0.35	17
15 September	0.27	15	0.37	19	0.10	10	0.29	7	0.06	16	0.36	11	0.10	10	0.00	10
1979																
16 May	0.90	10	0.69	13	1.00	6	1.00	4	1.00	20	0.46	28	0.93	15	0.22	18
8 June	1.00	2	1.00	4	1.00	7	0.50	4	1.00	10	0.95	21	1.00	4	0.80	5
24 June	1.00	9	0.69	16	1.00	2	1.00	1	1.00	9	0.87	23	1.00	2	1.00	8
18 July	1.00	1	0.71	7	1.00	2	1.00	4	0.67	3	0.82	17	1.00	3	0.60	10
10 August	0.33	3	1.00	2	1.00	1	1.00	3	0.50	2	0.67	9	1.00	1	0.75	8
31 August	0.30	10	0.50	4	0.00	1	-	0	0.00	1	0.86	7	0.40	5	0.17	6
20 September	0.35	20	0.00	5	0.00	0	-	0	0.25	8	0.20	5	0.50	6	0.00	6

[a] Date shown is mid-point of trapping period.

Table 45. Breeding activity of mature *P. maniculatus*. (Numbers of mature males and females captured and proportion in breeding condition during each trapping period are indicated for the summer periods of 1978 and 1979.)

	Aspen				Jack pine				Balsam poplar			
	Males		Females		Males		Females		Males		Females	
Date[a]	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978												
1 July	0.00	1	-	0	-	0	-	0	0.00	4	0.40	5
19 July	-	0	0.00	2	-	0	0.00	1	0.38	8	0.13	8
1 August	-	0	-	0	-	0	0.25	4	0.29	7	0.00	4
16 August	0.00	2	0.00	1	0.00	1	-	0	0.00	7	0.00	4
27 August	0.00	3	0.33	3	-	0	0.00	2	0.00	6	0.00	8
15 September	0.00	2	0.00	2	0.00	1	0.00	1	0.00	6	0.00	4
1979												
16 May	1.00	4	0.50	2	-	0	-	0	0.93	14	0.63	24
8 June	1.00	3	1.00	1	1.00	1	-	0	1.00	9	0.87	15
24 June	1.00	3	1.00	2	1.00	1	-	0	0.89	9	0.81	16
18 July	0.33	3	0.29	7	-	0	-	0	0.61	18	0.41	22
10 August	1.00	2	0.40	5	-	0	-	0	0.69	16	0.29	24
31 August	0.80	5	0.13	8	0.00	1	-	0	0.22	18	0.10	19
20 September	0.75	4	0.00	7	-	0	-	0	0.77	13	0.00	17

continued...

Table 45. Concluded.

	Poplar Creek				Black Spruce				Thickwood			
	Males		Females		Males		Females		Males		Females	
Date[a]	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978												
1 July	-	0	-	0	-	0	-	0	-	0	-	0
19 July	-	0	-	0	-	0	-	0	0.17	6	0.40	5
1 August	0.00	3	0.00	2	0.50	2	-	0	0.00	8	0.50	4
16 August	0.00	2	-	0	-	0	-	0	0.11	9	1.00	1
27 August	0.00	3	-	0	-	0	-	0	0.00	5	0.00	2
15 September	0.00	3	0.00	1	-	0	0.00	1	0.00	9	0.00	4
1979												
16 May	1.00	8	0.50	6	-	0	-	0	0.75	12	0.15	13
8 June	1.00	2	1.00	3	1.00	1	1.00	1	1.00	8	0.50	8
24 June	1.00	1	1.00	3	-	0	-	0	1.00	5	0.88	8
18 July	1.00	1	1.00	2	-	0	-	0	0.82	11	0.75	12
10 August	0.00	2	0.50	2	-	0	-	0	0.60	10	0.36	14
31 August	0.00	1	0.00	2	1.00	1	-	0	0.27	11	0.20	15
20 September	0.25	4	0.00	2	-	0	-	0	0.20	5	0.00	7

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[a] Date shown is mid-point of trapping period.

Table 46. Juvenile recruitment rates of *C. gapperi*. [Rates shown are expressed as the number of new immature animals (body weight < 10 g) captured per mature breeding female during each trapping period. The number of mature breeding females captured during each period is also indicated.]

Date[a]	Aspen		Jack pine		Willow		Balsam poplar		Poplar Creek		Black spruce		Thickwood		Tamarack	
	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N
1978 1 July	0.00	2	0.33	3	-	0	0.33	6	-	-	-	0	-	0	-	0
19 July	0.00	2	0.00	2	0.00	1	0.17	6	-	-	0.00	3	0.00	1	0.00	1
1 August	0.00	2	0.00	3	-	0	0.50	6	0.50	4	1.00	1	0.00	1	0.00	4
16 August	0.33	3	0.00	1	0.00	1	0.67	3	0.00	1	0.00	1	0.00	3	-	0
27 August	0.25	4	-	0	-	0	0.50	4	0.00	1	0.00	2	0.33	3	0.00	1
15 September	0.20	5	0.00	1	-	0	0.20	5	0.00	2	-	0	-	0	-	0
1979 16 May	0.00	6	0.00	5	0.00	1	0.00	4	0.00	5	0.00	7	0.00	5	0.00	11
8 June	0.00	3	0.00	4	-	0	0.00	3	0.00	3	0.00	4	0.00	2	0.14	7
24 June	0.20	5	0.40	5	-	0	0.33	3	0.25	4	0.63	6	0.00	2	0.00	6
18 July	0.00	11	0.33	6	0.00	1	0.33	6	-	0	1.25	4	0.00	4	0.25	4
10 August	0.57	7	0.60	5	0.00	1	0.14	7	0.00	1	0.00	3	0.00	6	0.00	2
31 August	0.00	4	0.33	3	0.00	1	0.20	5	0.00	2	0.00	1	0.50	2	0.67	3
20 September	1.00	2	0.00	1	0.00	2	0.50	2	0.00	2	-	0	0.00	2	-	0

[a] Dates shown are the mid-point of each trapping period.

Table 47. Juvenile recruitment rates of *M. pennsylvanicus*. [Rates shown are expressed as the number of new immature animals (body weight < 16 g) captured per mature breeding female during each trapping period. The number of mature breeding females captured during each period is also indicated.]

		Aspen		Jack pine		Willow		Balsam poplar		Poplar Creek		Black spruce		Thickwood		Tamarack	
	Date[a]	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N
1978	1 July	-	0	-	0	9.00	1	-	0	-	-	-	0	-	0	-	0
	19 July	-	0	-	0	-	0	0.00	2	-	-	0.00	2	0.00	5	0.00	3
	1 August	-	0	6.0	1	4.00	2	0.00	1	1.80	5	0.83	7	0.00	6	1.50	2
	16 August	3.0	0	0.5	2	4.50	2	0.00	1	0.57	7	2.80	5	0.71	7	1.75	4
	27 August	0.00	1	11.0	1	2.00	3	0.00	1	1.33	6	4.00	1	1.57	7	1.50	6
	15 September	-	0	-	0	-	0	-	0	0.29	7	1.50	2	2.25	4	-	0
1979	16 May	0.00	1	-	0	2.00	1	-	0	0.11	9	0.00	4	0.00	13	0.00	3
	8 June	-	0	-	0	-	0	-	0	0.50	4	0.00	2	0.00	20	0.00	4
	24 June	1.00	1	-	0	1.00	1	-	0	0.00	11	0.00	1	0.25	20	0.13	8
	18 July	0.00	2	-	0	0.50	4	0.00	3	0.20	5	0.25	4	0.43	14	0.17	6
	10 August	-	0	-	0	0.25	4	0.50	4	0.00	2	1.00	3	0.83	6	0.33	6
	31 August	1.00	1	-	0	0.00	1	1.25	4	0.50	2	-	0	0.17	6	0.00	1
	20 September	-	0	-	0	1.00	1	3.00	1	-	0	-	0	0.00	1	-	0

[a] Dates shown are the mid-point of each trapping period.

Table 48. Juvenile recruitment rates of *P. maniculatus*. [Rates shown are expressed as the number of new immature animals (body weight < 14 g) captured per mature breeding female during each trapping period. The number of mature breeding females captured during each period is also indicated.]

Date[a]		Aspen		Jack pine		Balsam poplar		Poplar Creek		Black spruce		Thickwood	
		Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N
1978	1 July	-	0	-	0	-	2	-	0	-	0	-	0
	19 July	-	0	-	0	3.00	1	-	0	-	0	1.50	2
	1 August	-	0	0.00	1	-	0	-	0	-	0	2.00	2
	16 August	-	0	-	0	-	0	-	0	-	0	0.00	1
	27 August	1.00	1	-	0	-	0	-	0	-	0	-	0
	15 September	-	0	-	0	-	0	-	0	-	0	-	0
1979	16 May	0.00	1	-	0	0.00	5	0.00	3	-	0	0.00	2
	8 June	0.00	1	-	0	0.31	13	0.00	3	0.00	1	0.00	4
	24 June	0.50	2	-	0	1.00	13	0.67	3	-	0	0.00	7
	18 July	0.00	2	-	0	0.78	9	0.00	2	-	0	0.89	9
	10 August	3.00	2	-	0	0.14	7	0.00	1	-	0	1.10	5
	31 August	0.00	1	-	0	1.50	2	-	0	-	0	0.67	3
	20 September	-	0	-	0	-	0	-	0	-	0	-	0

[a] Dates shown are the mid-point of each trapping period.

Table 49. Instantaneous relative growth rates. [Mean instantaneous growth rates (proportionate increase/day) were calculated for each species and is expressed as an adjusted mean growth rate for a hypothetical 25 g standard animal. Sample sizes are indicated.]

Date[a]	Aspen		Jack pine		Willow		Balsam Poplar		Poplar Creek		Black spruce		Thickwood		Tamarack	
	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N
C. gapperi																
1978 11 July	0.010	12	0.007	9	-0.007	3	0.001	51	-	0	0.001	9	-	0	0.001	10
9 August	0.009	14	0.006	9	0.007	8	0.001	64	0.004	33	0.002	24	0.004	8	0.002	21
10 September	0.000	38	-0.001	20	0.002	19	0.002	106	0.003	53	0.002	47	0.000	15	0.001	61
10 October	0.000	88	0.000	35	-0.002	42	-0.001	119	-0.003	58	-0.003	50	0.000	24	-0.002	96
3 November	-0.006	46	-0.002	20	-0.004	32	0.000	56	0.001	19	-0.001	28	-0.004	8	-0.001	47
1979 8 June	0.004	27	0.007	10	-	2	0.002	10	0.003	8	0.002	21	0.000	3	0.002	31
18 July	0.001	18	0.001	8	0.002	3	0.006	12	-	0	0.004	12	-0.001	7	0.002	15
31 August	0.002	27	0.001	14	0.002	4	0.001	35	-0.001	3	0.002	12	-0.001	6	0.000	15
13 October	0.001	30	-0.001	24	-0.002	20	0.000	36	-	0	0.000	12	-	0	-0.001	21
M. pennsylvanicus																
1978 11 July	0.000	4	0.021	4	0.006	19	-[b]	1	-	0	0.006	13	0.005	17	0.004	15
9 August	0.008	7	0.021	5	0.006	34	-	2	0.005	37	0.008	44	0.001	35	0.005	52
10 September	0.002	7	0.010	19	0.003	66	-	1	0.004	80	0.002	65	0.005	75	0.004	76
10 October	0.005	4	-0.003	14	0.002	61	-	0	0.000	100	-0.003	42	-0.001	67	0.001	65
3 November	-	0	-0.003	4	0.005	36	-	1	-0.002	47	0.001	13	-0.001	25	0.000	26
1979 8 June	-	2	-[b]	0	0.004	5	-	0	-	0	0.005	7	0.003	33	0.002	9
18 July	-	1	-	0	0.000	6	-	1	-	0	-0.005	3	-0.001	5	0.000	7
31 August	-	0	-	0	0.006	18	-0.001	10	0.000	10	-	0	-0.004	3	0.000	6
13 October	-	0	-	0	-0.001	22	0.002	4	0.002	10	-	0	-	0	0.000	8

continued...

Table 49. Concluded.

Date[a]	Aspen		Jack pine		Willow		Balsam Poplar		Poplar Creek		Black spruce		Thickwood		Tamarack	
	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N	Rate	N
P. maniculatus																
1978 11 July	0.005	6	0.007	3	-[b]	0	0.000	34	-	0	-	0	0.002	20	-	0
9 August	0.004	16	0.005	5	-	0	0.000	41	0.003	6	0.004	3	0.004	45	-	0
10 September	0.001	22	0.002	3	-	0	0.004	33	0.003	13	-0.001	4	0.003	45	-	0
10 October	0.001	16	0.004	3	-	0	0.001	20	0.003	22	0.003	4	-0.001	53	-	0
3 November	0.001	9	0.000	3	-	0	-	0	-	0	-	0	0.000	3	-	0
1979 8 June	0.000	6	-[b]	0	-[b]	0	0.000	30	0.002	6	-[b]	0	0.000	24	-	0
18 July	0.006	7	-	0	-	0	0.004	53	-	0	-	0	0.002	21	-	0
31 August	0.003	19	-	0	-	0	0.001	55	0.002	3	-	0	0.000	33	-	0
13 October	0.003	7	-	0	-	0	0.001	24	-	0	-	0	0.000	13	-	0

[a] Mid-point of trapping dates included in the calculation of instantaneous relative growth rates are indicated.

[b] No or too few animals captured for calculation of instantaneous relative growth rates.

11.3 SMALL RODENT HABITAT USE

11.3.1 Principal Components Analysis of Vegetation on the Small Rodent Study Areas

A factor (principal components) analysis was used to reduce the large number of habitat variables to a smaller number of independent variables. Based on the results of the vegetation sampling program in 1978 and 1979, a total of 216 variables were defined; these included measures of the percent horizontal ground cover of 168 plant species or species groups, estimates of the stem densities of 39 tree and shrub species, estimates of the cumulative vertical cover in the six 25 cm vertical increments, and estimates of the height (above ground) of the zone of densest foliage for the three major plant species in each sampling quadrat. Many of these variables were non-zero in only a few cases on one or two study areas. Consequently, relationships of mouse abundance to these variables were unlikely to be detectable even if real. Because of this, plus the need to reduce the number of variables to a more manageable value, only those variables recorded as non-zero in at least 20 samples (for 1978 and 1979 data combined) were included in the factor analysis. This reduced the number of variables considered to 89. All estimates of stem densities were transformed using a log (x + 1) transformation (where x equals the untransformed estimate of stem density) prior to the factor analysis.

Because no or extremely few *P. maniculatus* were present on the Willow, Tamarack, and Black Spruce study areas, two separate factor analyses were performed; one included vegetation information from all eight study areas (to be used in further analyses with *C. gapperi* and *M. pennsylvanicus* populations in natural areas), whereas the other excluded the vegetation information from the Willow, Tamarack, and Black Spruce study areas (to be used in further analyses with *P. maniculatus* populations in natural areas).

Factor analyses were run on the combined vegetation data from 1978 and 1979 using the BMDP4M computer program (Dixon and Brown 1979). By combining the two years of vegetation data, changes in the distribution and abundance of small rodents between years can be more effectively evaluated. Both factor analyses were performed by a standard method--a principal components analysis followed by Varimax (orthogonal) rotation of those principal components whose eigenvalues exceeded 1.0. Habitat factors with eigenvaulues less than 1.5 following rotation of the original principal components were not included in the stepwise multiple regression analyses because very few habitat variables characterized these factors (i.e., 1 to 3 variables per factor) and almost all such variables had already been included in other factors whose eigenvalues were greater than 1.5.

The eight-area and the five-area factor analysis both reduced the 89 habitat variables to a set of 17 independent factors whose eigenvalues were greater than 1.5. Rotated factor loadings (correlation coefficients between the 89 habitat variables and the 17 habitat factors following Varimax rotation) for the eight-area and the six-area factor analyses are shown in Tables 50 and 51, respectively. Biological interpretations of the 17 habitat factors are summarized in Tables 17 and 18.

11.3.2 Indices of Habitat Quality

Six indices of habitat quality, peak MNAs, expected CTNs, habitat preferences, dispersal indices, reproductive success and condition, were used to compare the suitabilities of the major habitat types for small mammals. To permit visual comparisons of each habitat type, each of the six indices were ranked among the eight habitat types studied; aspen, jack pine, balsam poplar, black spruce, and tamarack forest, willow shrub and successional areas.

Values of both peak MNAs and expected CTNs were plotted as the actual values reported. The remaining four indices were ranked on ordinal scales.

Dispersal indices were ranked on a scale of 1 to 4. Value equivalents were: 1 = limited dispersal; 2 = low; 3 = moderate; and 4 = high. Moderate and high mortality also were ranked as 3 and 4, respectively.

Table 50. Factor loadings for the eight study area factor analysis. [Only the correlations between the original 89 variables and the 17 factors whose absolute values were ≥ 0.250 are shown. Only factors with VP's (total variance in vegetation structure that was explained by the factor) that exceeded 1.5 were included in the SMR. The variable prefixes GC, VC, and ST refer to percent ground cover, percent vertical cover, and density of stems/16 m^2 respectively.]

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10	Factor 11	Factor 12	Factor 13	Factor 14	Factor 15	Factor 16	Factor 17
ST - *A. alnifolia*	0.835																
GC - *A. alnifolia*	0.797																
ST - *L. dioica*	0.793																
ST - *S. canadensis*	0.779																
VC - *A. alnifolia*	0.767																
GC - *L. ochroleucus*	0.708																
ST - *S. albus*	0.665																
GC - *V. myrtilloides*	0.655																
GC - *L. borealis*	0.569																0.440
GC - *S. canadensis*	0.565																
ST - *R. oxyacanthoides/ hirtellum*		0.830															
ST - *R. triste*		0.695															
GC - *C. alpina*		0.690															
ST - *C. stolonifera*		0.646											0.472				
ST - *R. americanum*		0.626															
ST - *Alnus* spp.		0.596								0.301							
GC - *R. oxyacanthoides/ hirtellum*		0.591															
ST - *R. melanolasius*		0.546								0.447							
VC - *Equisetum* spp.		0.531														0.424	
SC - *L. groenlandicum*			0.839														
VC - *L. groenlandicum*			0.822														
GC - *R. chamaemorus*			0.738														
GC - *V. vitis-idaea*			0.714														
ST - *P. mariana*			0.642														
GC - *P. mariana*			0.641														
GC - Moss			0.549			0.480	0.287										
VC - 75 to 100 cm				0.901													
VC - 100 to 125 cm				0.879													
VC - 50 to 75 cm				0.827													
VC - 125 to 150 cm				0.816										-0.263			
VC - 25 to 50 cm				0.662										0.377			
GC - *V. caespitosum*					0.823												
GC - *Cladonia* spp.					0.775												

continued...

Table 50. Continued.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10	Factor 11	Factor 12	Factor 13	Factor 14	Factor 15	Factor 16	Factor 17
VC - *V. caespitosum*					0.742												
ST - *P. tremuloides*					0.740												
GC - *P. tremuloides*					0.614												
VC - *M. canadense*						0.735											
ST - *L. laricina*			0.360			0.699											
GC - *M. canadense*						0.687											
GC - *B. glandulosa*						0.622	0.315				0.403						
VC - *B. glandulosa*						0.582	0.352				0.393						
ST - *B. glandulosa*						0.576	0.403				0.305						
GC - *G. boreale*						0.540											
GC - *Salix* spp.							0.813										
VC - *Salix* spp.							0.780										
GC - *R. acaulis*							0.646				0.260						
ST - *Salix* spp.							0.640										
GC - *H. umbellatum*								0.744						0.257			
GC - *Achillea* spp.								0.740									
GC - *Aster* spp.								0.723									
GC - *V. americana*								0.619									
GC - *Rosa* spp.	0.302								0.784								
VC - *Rosa* spp.									0.761								0.263
ST - *Rosa* spp.	0.333								0.577								
VC - *R. melanolasius*		0.324								0.795							
GC - *R. melanolasius*										0.785							
GC - *P. fruticosa*							0.285				0.703						
GC - *F. virginiana*											0.568						
GC - *V. uliginosum*							0.333				0.535						
GC - *Vibirnum* spp.												0.836					
ST - *Viburnum* spp.												0.801					
VC - *C. stolonifera*		0.383											0.821				
GC - *C. stolonifera*		0.377											0.819				
VC - Grass/Sedge														0.641			
GC - Grass/Sedge		-0.273	-0.385											0.516			
VC - *E. angustifolium*															0.835		
GC - *E. angustifolium*															0.704		
GC - *Equisetum* spp.																0.813	
GC - *Equisetum* spp.		0.501														0.595	0.564
ST - *P. glauca*																	0.555
GC - *C. canadensis*	0.343																
VC - *A. uva-ursi*					0.432												
GC - *A. uva-ursi*	0.281																
GC - *P. asarifolia*						0.332											
GC - *M. alba/ officinalis* spp.																	
VC - 0 to 25 cm				0.482	-0.296									0.445			

continued...

Table 50. Concluded.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10	Factor 11	Factor 12	Factor 13	Factor 14	Factor 15	Factor 16	Factor 17
GC - Deadfall		0.489															
ST - *P. balsamifera*		0.293						0.483									
GC - *Petasites* spp.							0.267	0.375	0.323								
GC - *V. rugulosa*		0.354															
GC - *P. major*								0.457		-0.258							
GC - *G. boreale*	0.304								0.270		0.325						
GC - *G. triflorum*		0.420															
GC - *R. pubescens*									0.384								
VC - Litter			-0.288	0.360										-0.465			
GC - Litter		0.460										0.311				-0.310	
VP	6.570	6.217	4.716	4.177	4.150	3.879	3.419	3.391	2.423	2.286	2.273	2.100	1.925	1.798	1.736	1.716	1.659

Table 51. Factor loadings for the six study area factor analysis. [Only the correlations between the original 89 variables and the 17 factors whose absolute values were ≥ 0.250 are shown. Only factors with VP's (total variance in vegetation structure that was explained by the factor) that exceeded 1.5 were included in the SMR. The variable prefixes GC, VC, and ST refer to percent ground cover, percent vertical cover, and density of stems/16 m^2 respectively.]

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10	Factor 11	Factor 12	Factor 13	Factor 14	Factor 15	Factor 16	Factor 17
ST - *L. dioica*	0.826																
ST - *A. alnifolia*	0.807																
GC - *L. ochroleucus*	0.752																
ST - *S. canadensis*	0.748								0.255								
GC - *A. alnifolia*	0.707																
GC - *V. myrtilloides*	0.696															0.252	
ST - *S. albus*	0.672																
GC - *L. borealis*	0.659																
VC - *A. alnifolia*	0.651																
ST - *R. oxyacanthoides/ hirtellum*		0.825															
ST - *R. triste*		0.681															
GC - *C. alpina*		0.672															
ST - *C. stolonifera*		0.622										0.470					
ST - *R. americanum*		0.618															
GC - *R. oxyacanthoides/ hirtellum*		0.598															
ST - *Alnus* spp.		0.572						0.270									
GC - Litter		0.571							0.383								
GC - Deadfall		0.542															
GC - *Cladonia/ Cladina* spp.			0.830														
GC - *V. caespitosum*			0.821														
ST - *P. tremuloides*			0.757														
VC - *V. caespitosum*			0.705			0.380											
GC - *A. uva-ursi*	0.338		0.675														
VC - *A. uva-ursi*			0.597														
GC - *P. tremuloides*			0.588												0.276		
GC - *M. canadense*	0.507		0.510											0.311			
VC - 100 to 125 cm				0.890													
VC - 75 to 100 cm				0.885													
VC - 125 to 150 cm				0.839													
VC - 50 to 75 cm				0.828													
VC - 25 to 50 cm				0.648							0.393						
GC - *Aster* spp.					0.739												

continued...

Table 51. Continued.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10	Factor 11	Factor 12	Factor 13	Factor 14	Factor 15	Factor 16	Factor 17
GC - *H. umbellatum*					0.711						0.293						
GC - *Achillea* spp.					0.700												
GC - *V. americana*					0.652												
GC - *Salix* spp.					0.512												0.347
VC - *L. groenlandicum*						0.818											
GC - *L. groenlandicum*						0.752											
ST - *L. laricina*						0.705											
ST - *B. glandulosa*						0.510				0.387						0.426	
GC - Moss						0.509				0.275							
GC - *Rosa* spp.							0.805										
VC - *Rosa* spp.							0.772										
ST - *Rosa* spp.	0.315						0.632										
GC - *R. melanolasius*								0.805									
VC - *R. melanolasius*		0.286						0.800									
GC - *Viburnum* spp.									0.825								
ST - *Viburnum* spp.									0.818								
GC - *B. glandulosa*										0.933							
VC - *B. glandulosa*										0.917							
VC - Grass/Sedge											0.750						
GC - Grass/Sedge		-0.335									0.625						
GC - *C. stolonifera*		0.354										0.797					
VC - *C. stolonifera*		0.363										0.796					
VC - *E. angustifolium*													0.858				
GC - *E. angustifolium*		-0.255											0.747				
GC - *V. vitis-idaea*														0.779			
GC - *V. uliginosum*						0.359								0.717			
GC - *Equisetum sylvaticum*															0.710		
GC - *Equisetum* spp.		0.479													0.566		
VC - *Equisetum* spp.		0.509													0.523		
GC - *P. mariana*																0.794	
VC - *Salix* spp.																	0.789
GC - *P. asarifolia*																	
GC - *M. alba/ officinalis*																	
GC - *S. canadensis*	0.459																
GC - *Petasites* spp.					0.468		0.290										
GC - *G. boreale*	0.449						0.271										
ST - *P. balsamifera*					0.409												0.454
ST - *P. glauca*	0.287															0.477	
ST - *P. mariana*																	
GC - *R. acaulis*																	0.311
ST - *Salix* spp.		-0.316			0.364								-0.252				
GC - *O. microcarpus*																	

continued...

Table 51. Concluded.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10	Factor 11	Factor 12	Factor 13	Factor 14	Factor 15	Factor 16	Factor 17
GC - *C. canadensis*	0.454															0.251	
GC - *G. boreale*		0.424															0.296
GC - *P. virginiana*																	
GC - *V. rugulosa*		0.291															0.364
GC - *P. fruticosa*																	
VC - *N. canadensis*			0.401											0.488		-0.267	
GC - *R. chamaemorus*																	
VC - 0 to 25 cm		0.281	-0.275	0.462				0.253			0.464						
GC - *P. major*					0.384			-0.263									
VC - Litter		-0.266	-0.261	0.470							-0.439						
ST - *R. melanolasius*	-0.319	0.499	-0.268					0.453									
GC - *R. pubescens*							0.332										
VP	7.051	6.246	5.261	4.409	3.622	3.003	2.579	2.402	2.270	2.225	2.047	1.981	1.876	1.817	1.811	1.765	1.637

Habitat preferences were ranked on a scale of 1 to 5. Value equivalents were: 1 = major tree and shrub components avoided; 2 = major tree or shrub components avoided; 3 = major tree and shrub components neutral; 4 = major tree or shrub components preferred; 5 = major tree and shrub components preferred.

Reproductive success included indices of breeding activity, pregnancy rates, and juvenile recruitment, and were ranked on a scale of 1 (= lowest) to 8 (1 = highest). Each component of reproductive success was ranked among the eight study areas. The mean rank for the three components of reproductive success on each area was then calculated and was used as an overall rating of reproductive success.

The nutritional condition index included Le Cren's index of condition and the fat index for snap-trapped animals in each major forest cover type discussed above. Each component of the nutritional condition index was ranked on a scale of 1 (1 = poorest condition) to 8 (= best condition). The mean rank of the two components was calculated and was used as an overall rating of nutritional condition.

Table 52. SMR analysis of the abundance and distribution of *C. gapperi* in 1978. [See Table 17 for explanation of variable names. Multiple r-square = 0.5374; standard error of estimate = 0.0412; df = 11,228; F-ratio = 23.46; $P \leq 0.001$. CTN of *C. gapperi* were transformed by taking the square root of (CTN + 1).]

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		-0.114				
Balsam poplar understory	1	0.034	0.003	0.2887	0.2887	***
Dogwood shrub	2	0.010	0.002	0.3446	0.0559	***
Successional cover[b]	3	0.055	0.012	0.3816	0.0370	***
Aspen understory	4	-0.010	0.003	0.4165	0.0349	***
Willow-birch shrub	5	-0.010	0.003	0.4441	0.0276	***
Fireweed cover	6	-0.007	0.002	0.4657	0.0216	***
Raspberry shrub	7	0.008	0.003	0.4805	0.0148	***
Dwarf birch shrub	8	-0.005	0.003	0.4943	0.0139	***
Viburnum shrub	9	0.007	0.003	0.5069	0.0126	***
Rose understory[b]	10	0.031	0.012	0.5178	0.0108	***
Tamarack understory	11	-0.008	0.003	0.5284	0.0107	***
Dense vertical cover	12	0.006	0.003	0.5374	0.0090	***

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

[b] Variables transformed using a $\sqrt{x+4}$ transformation, where x = factor loading for each sample.

Table 53. Mean factor scores for the eight study areas in 1978. (Mean factor scores and 1 S.E. are indicated for each factor based on the factor scores for each of the 30 samples on each study area. Factor scores are from the eight-study area factor analysis.)

		Study Areas							
	Factor	Jack pine	Aspen	Willow	Balsam poplar	Poplar Creek Cutline	Black Spruce	Thickwood Cutline	Tamarack
1.	Aspen understory	2.47 ± 0.18	-0.20 ± 0.10	-0.34 ± 0.03	-0.38 ± 0.05	-0.44 ± 0.06	-0.22 ± 0.03	-0.67 ± 0.03	-0.37 ± 0.02
2.	Balsam poplar understory	-0.32 ± 0.09	-0.31 ± 0.03	-0.23 ± 0.06	2.88 ± 0.14	-0.38 ± 0.12	-0.46 ± 0.04	-0.92 ± 0.09	-0.32 ± 0.06
3.	Black spruce forest	-0.26 ± 0.04	-0.45 ± 0.05	-0.39 ± 0.07	-0.34 ± 0.03	-0.43 ± 0.05	1.72 ± 0.17	-0.91 ± 0.08	0.51 ± 0.18
4.	Dense vertical cover	0.01 ± 0.14	-0.18 ± 0.20	-0.06 ± 0.20	0.39 ± 0.15	0.17 ± 0.18	0.47 ± 0.15	0.26 ± 0.32	0.24 ± 0.17
5.	Jack pine understory	-0.23 ± 0.10	1.92 ± 0.12	-0.46 ± 0.06	-0.37 ± 0.06	-0.50 ± 0.08	0.12 ± 0.10	-0.69 ± 0.10	-0.46 ± 0.04
6.	Tamarack understory	-0.17 ± 0.06	-0.20 ± 0.05	-0.09 ± 0.09	-0.25 ± 0.05	-0.42 ± 0.07	-0.50 ± 0.05	-0.87 ± 0.06	1.89 ± 0.26
7.	Willow-birch scrub	-0.15 ± 0.09	-0.21 ± 0.08	1.61 ± 0.24	-0.31 ± 0.04	-0.32 ± 0.13	0.06 ± 0.19	-0.69 ± 0.12	-0.17 ± 0.16
8.	Successional cover	-0.01 ± 0.14	-0.30 ± 0.03	-0.51 ± 0.06	-0.04 ± 0.08	1.99 ± 0.28	-0.12 ± 0.08	-0.62 ± 0.05	-0.25 ± 0.03
9.	Rose understory	0.12 ± 0.21	-0.23 ± 0.08	-0.49 ± 0.05	0.15 ± 0.23	0.21 ± 0.29	0.17 ± 0.13	0.05 ± 0.15	-0.24 ± 0.04
10.	Raspberry shrub	-0.07 ± 0.06	-0.16 ± 0.04	0.03 ± 0.07	0.68 ± 0.35	-0.49 ± 0.23	-0.11 ± 0.05	-0.09 ± 0.18	-0.15 ± 0.05
11.	Dwarf birch shrub	-0.14 ± 0.11	-0.17 ± 0.07	1.39 ± 0.31	-0.24 ± 0.09	-0.39 ± 0.12	-0.05 ± 0.11	-0.53 ± 0.03	-0.08 ± 0.12
12.	*Viburnum* shrub	0.37 ± 0.40	-0.10 ± 0.03	0.23 ± 0.04	0.67 ± 0.23	0.06 ± 0.21	-0.16 ± 0.04	-0.33 ± 0.06	-0.02 ± 0.04
13.	Dogwood shrub	-0.13 ± 0.08	-0.06 ± 0.06	-0.25 ± 0.04	0.30 ± 0.46	0.52 ± 0.29	0.09 ± 0.04	-0.18 ± 0.07	-0.04 ± 0.03
14.	Grass/sedge cover	-0.14 ± 0.09	-0.11 ± 0.07	0.38 ± 0.11	-0.34 ± 0.11	0.62 ± 0.28	-0.19 ± 0.11	-1.45 ± 0.30	-0.03 ± 0.08
15.	Fireweed cover	0.89 ± 0.44	-0.20 ± 0.08	0.13 ± 0.08	-0.01 ± 0.09	0.11 ± 0.26	-0.10 ± 0.07	0.16 ± 0.17	-0.04 ± 0.07
16.	*Equisetum* cover	-0.10 ± 0.07	-0.22 ± 0.09	-0.66 ± 0.05	-0.19 ± 0.15	-0.05 ± 0.17	0.30 ± 0.16	0.50 ± 0.30	0.89 ± 0.21
17.	White spruce understory	-0.09 ± 0.25	0.05 ± 0.15	-0.44 ± 0.07	0.28 ± 0.13	-0.18 ± 0.11	0.11 ± 0.27	-0.47 ± 0.10	0.15 ± 0.15

Table 54. SMR analysis of the abundance and distribution of *C. gapperi* in 1979. [See Table 17 for explanation of variable names. Multiple r-square = 0.2001; standard error of estimate = 0.0390; df = 4,233; F-ratio = 14.57; $P \leq 0.001$. CTN of *C. gapperi* were transformed by taking the log of (CTN + 1).]

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.042				
Balsam poplar understory	1	-0.012	0.002	0.0717	0.0717	***
Aspen understory	2	-0.012	0.003	0.1273	0.0556	***
Successional cover	3	-0.010	0.003	0.1732	0.0458	***
Viburnum shrub	4	-0.007	0.003	0.2001	0.0269	**

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 55. Mean factor scores for the eight study areas in 1979. (Mean factor scores and 1 S.E. are indicated for each factor based on the factor scores for each of the 30 samples on each study area. Factor scores are from the eight-study area factor analysis.)

		Study Areas							
	Factor	Jack pine	Aspen	Willow	Balsam poplar	Poplar Creek Cutline	Black Spruce	Thickwood Cutline	Tamarack
1.	Aspen understory	2.15 ± 0.22	-0.29 ± 0.10	-0.24 ± 0.03	-0.08 ± 0.05	-0.30 ± 0.05	-0.27 ± 0.04	-0.57 ± 0.05	-0.25 ± 0.03
2.	Balsam poplar understory	-0.28 ± 0.08	-0.10 ± 0.05	-0.24 ± 0.09	2.58 ± 0.17	-0.26 ± 0.09	-0.24 ± 0.03	-0.34 ± 0.11	-0.05 ± 0.07
3.	Black spruce forest	-0.23 ± 0.05	-0.36 ± 0.09	-0.48 ± 0.08	-0.24 ± 0.04	-0.42 ± 0.04	2.15 ± 0.16	-0.47 ± 0.04	0.60 ± 0.23
4.	Dense vertical cover	-0.31 ± 0.12	-0.25 ± 0.15	0.68 ± 0.17	0.35 ± 0.14	-0.27 ± 0.16	-0.03 ± 0.14	-0.97 ± 0.09	-0.48 ± 0.12
5.	Jack pine understory	-0.36 ± 0.10	2.44 ± 0.21	-0.36 ± 0.06	-0.19 ± 0.05	-0.30 ± 0.07	0.15 ± 0.13	-0.28 ± 0.08	-0.45 ± 0.04
6.	Tamarack understory	-0.04 ± 0.07	0.16 ± 0.08	-0.03 ± 0.10	-0.21 ± 0.05	-0.42 ± 0.06	-0.44 ± 0.10	-0.61 ± 0.03	2.18 ± 0.24
7.	Willow-birch scrub	-0.37 ± 0.09	-0.29 ± 0.09	1.71 ± 0.22	-0.33 ± 0.04	-0.10 ± 0.15	-0.24 ± 0.19	-0.37 ± 0.07	0.17 ± 0.15
8.	Successional cover	-0.41 ± 0.07	-0.22 ± 0.03	-0.26 ± 0.12	-0.34 ± 0.07	1.95 ± 0.26	-0.20 ± 0.05	-0.54 ± 0.09	-0.12 ± 0.04
9.	Rose understory	0.65 ± 0.26	-0.28 ± 0.08	-0.33 ± 0.08	0.10 ± 0.27	-0.03 ± 0.22	-0.08 ± 0.11	0.40 ± 0.25	-0.17 ± 0.06
10.	Raspberry shrub	-0.21 ± 0.07	-0.21 ± 0.05	-0.34 ± 0.10	0.54 ± 0.40	0.12 ± 0.21	0.00 ± 0.04	0.64 ± 0.22	-0.17 ± 0.06
11.	Dwarf birch shrub	0.18 ± 0.12	-0.04 ± 0.10	1.10 ± 0.39	-0.14 ± 0.08	-0.20 ± 0.13	0.13 ± 0.13	-0.11 ± 0.09	-0.72 ± 0.13
12.	*Viburnum* shrub	0.18 ± 0.39	-0.04 ± 0.04	-0.24 ± 0.06	0.04 ± 0.27	-0.17 ± 0.11	0.00 ± 0.05	-0.34 ± 0.06	-0.17 ± 0.04
13.	Dogwood shrub	-0.03 ± 0.09	-0.18 ± 0.05	0.00 ± 0.05	0.43 ± 0.42	-0.21 ± 0.10	-0.11 ± 0.05	-0.11 ± 0.08	-0.06 ± 0.04
14.	Grass/sedge cover	0.21 ± 0.11	-0.09 ± 0.07	0.15 ± 0.17	0.01 ± 0.14	0.91 ± 0.31	-0.02 ± 0.09	0.28 ± 0.13	-0.19 ± 0.09
15.	Fireweed cover	-0.41 ± 0.16	-0.02 ± 0.10	-0.20 ± 0.08	-0.47 ± 0.08	-0.39 ± 0.14	-0.21 ± 0.08	0.84 ± 0.27	-0.09 ± 0.06
16.	*Equisetum* cover	-0.20 ± 0.08	-0.36 ± 0.10	-0.20 ± 0.08	-0.02 ± 0.16	-0.08 ± 0.18	-0.54 ± 0.08	1.10 ± 0.33	-0.18 ± 0.08
17.	White spruce understory	1.33 ± 0.31	0.03 ± 0.16	-0.26 ± 0.10	-0.31 ± 0.15	-0.14 ± 0.10	0.19 ± 0.21	-0.12 ± 0.10	-0.12 ± 0.13

Table 56. Forced SMR analysis of the abundance and distribution of *C. gapperi* in 1979. (All predictor variables found to be significant in 1978 were included in this reanalysis of the 1979 data. See Table 17 for explanation of variable names. Multiple r-square = 0.2518; standard error of the estimate = 0.0398; df = 12,227; F-ratio = 6.37; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.042				
Balsam poplar understory	1	0.012	0.003	0.0826	0.0826	***
Dogwood shrub	2	0.008	0.003	0.0919	0.0092	NS
Successional cover	3	0.009	0.003	0.1318	0.0399	***
Aspen understory	4	-0.009	0.003	0.1697	0.0379	***
Willow birch shrub	5	-0.008	0.003	0.1909	0.0212	***
Fireweed cover	6	0.001	0.003	0.1909	0.0000	NS
Raspberry shrub	7	0.006	0.003	0.2093	0.0184	***
Dwarf birch shrub	8	-0.008	0.003	0.2353	0.0260	***
Viburnum shrub	9	-0.002	0.003	0.2363	0.0010	NS
Rose understory	10	0.004	0.003	0.2454	0.0091	**
Tamarack understory	11	0.002	0.003	0.2463	0.0009	NS
Dense vertical cover	12	0.004	0.003	0.2518	0.0055	NS

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 57. SMR analysis of the abundance and distribution of *M. pennsylvanicus* in 1978. (See Table 17 for explanation of variable names. Multiple r-square = 0.5507; standard error of estimate = 0.0407; df = 8,231; F-ratio = 35.40; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P[a]
Constant		0.065				
Successional cover	1	0.023	0.003	0.1365	0.1365	***
Balsam poplar understory	2	-0.023	0.003	0.2759	0.1395	***
Jack pine understory	3	-0.023	0.003	0.3980	0.1221	***
Aspen understory	4	-0.016	0.003	0.4613	0.0633	***
Equisetum cover	5	0.011	0.003	0.4916	0.0303	***
Grass/sedge cover	6	0.009	0.003	0.5194	0.0278	***
White spruce understory	7	-0.009	0.003	0.5398	0.0204	**
Black spruce forest	8	0.007	0.003	0.5507	0.0109	*

[a] Two-sided signifance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 58. SMR analysis of the abundance and distribution of *M. pennsylvanicus* in 1979. (See Table 17 for explanation of variable names. Multiple r-square = 0.2691; standard error of estimate = 0.0379; df = 7,232; F-ratio = 11.30; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.034				
Successional cover	1	0.016	0.003	0.1025	0.1025	***
Grass/sedge cover	2	0.011	0.003	0.1583	0.0558	***
Equisetum cover	3	-0.008	0.003	0.1786	0.0203	**
Tamarack understory	4	-0.007	0.002	0.2016	0.0230	**
Jack pine understory	5	-0.005	0.002	0.2222	0.0206	*
Balsam poplar understory	6	0.006	0.002	0.2394	0.0172	*
Dogwood shrub	7	0.006	0.003	0.2542	0.0148	*
Viburnum cover	8	0.006	0.003	0.2691	0.0149	*

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 59. Forced SMR analysis of the abundance and distribution of *M. pennsylvanicus* in 1979. (All predictor variables found to be significant in 1978 were included in this reanalysis of the 1979 data. See Table 17 for explanation of variable names. Multiple r-square = 0.0872; standard error of the regression = 0.343; df = 8,231; F-ratio = 2.76; 0.005 > P > 0.001.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P[a]
Constant		0.029				
Successional cover	1	-0.006	0.002	0.0210	0.0210	**
Balsam poplar understory	2	-0.005	0.002	0.0463	0.0253	**
Jack pine understory	3	0.000	0.002	0.0463	0.0000	NS
Aspen understory	4	0.001	0.002	0.0471	0.0008	NS
Equisetum cover	5	-0.006	0.002	0.0821	0.0350	***
Grass/sedge cover	6	-0.002	0.003	0.0853	0.0032	NS
White spruce understory	7	0.001	0.002	0.0872	0.0019	NS
Black spruce	8	0.000	0.002	0.0872	0.0000	NS

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 60. SMR analysis of the abundance and distribution of *P. maniculatus* in 1978. (See Table 18 for explanation of variable names. Multiple r-square = 0.4840; standard error or estimate = 0.0415; df = 7,140; F-ratio = 18.76; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.058				
Balsam poplar understory	1	0.031	0.004	0.1681	0.1681	***
Jack pine understory	2	-0.016	0.004	0.2509	0.0828	***
Successional cover	3	-0.015	0.003	0.3290	0.0781	***
Aspen understory	4	-0.012	0.003	0.3845	0.0554	***
Equisetum cover	5	0.011	0.004	0.4275	0.0430	**
Grass/sedge cover	6	-0.009	0.003	0.4584	0.0309	**
Dense vertical cover	7	0.008	0.003	0.4840	0.0255	*

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 61. Mean factor scores for study areas included in the five-study area factor analysis in 1978. (Mean factor scores and 1 S.E. are indicated for each factor based on the factor scores for each of the 30 samples on each area. The Willow, Black spruce, and Tamarack study areas were not included in the analysis because of the extremely low numbers of animals captured in these areas.)

		Study Areas				
	Factor	Jack pine	Aspen	Balsam poplar	Poplar Creek cutline	Thickwood cutline
1.	Aspen understory	1.87 ± 0.12	-0.35 ± 0.06	-0.34 ± 0.05	-0.46 ± 0.05	-0.72 ± 0.03
2.	Balsam poplar understory	-0.28 ± 0.08	-0.38 ± 0.04	1.37 ± 0.11	-0.42 ± 0.09	-1.02 ± 0.09
3.	Jack pine understory	-0.14 ± 0.10	1.42 ± 0.10	-0.32 ± 0.06	-0.53 ± 0.08	-0.78 ± 0.08
4.	Dense vertical cover	0.07 ± 0.14	-0.12 ± 0.20	0.42 ± 0.15	0.24 ± 0.18	0.41 ± 0.32
5.	Successional cover	-0.03 ± 0.14	-0.35 ± 0.04	-0.21 ± 0.08	1.38 ± 0.26	-0.70 ± 0.05
6.	Tamarack forest	0.05 ± 0.07	0.33 ± 0.23	-0.14 ± 0.04	-0.13 ± 0.04	-0.26 ± 0.03
7.	Rose understory	-0.04 ± 0.17	-0.30 ± 0.08	-0.01 ± 0.20	-0.05 ± 0.22	-0.14 ± 0.14
8.	Raspberry shrub	-0.05 ± 0.08	-0.18 ± 0.04	0.55 ± 0.28	-0.41 ± 0.18	-0.22 ± 0.16
9.	*Viburnum* shrub	0.27 ± 0.29	-0.02 ± 0.03	0.58 ± 0.18	0.03 ± 0.17	-0.41 ± 0.07
10.	Dwarf birch shrub	0.05 ± 0.14	-0.09 ± 0.05	0.00 ± 0.03	-0.16 ± 0.03	-0.16 ± 0.03
11.	Grass/sedge cover	-0.05 ± 0.08	-0.08 ± 0.07	-0.23 ± 0.09	0.54 ± 0.26	-1.04 ± 0.22
12.	Dogwood shrub	-0.21 ± 0.08	-0.06 ± 0.07	0.14 ± 0.36	0.29 ± 0.23	-0.19 ± 0.08
13.	Fireweed cover	0.76 ± 0.35	-0.26 ± 0.07	-0.05 ± 0.06	0.04 ± 0.22	0.07 ± 0.15
14.	Black spruce ground cover	-0.30 ± 0.11	-0.44 ± 0.06	0.01 ± 0.03	-0.04 ± 0.05	-0.22 ± 0.04
15.	*Equisetum* cover	-0.21 ± 0.09	-0.31 ± 0.12	-0.20 ± 0.14	-0.27 ± 0.16	0.40 ± 0.26
16.	Black spruce - white spruce transition	-0.23 ± 0.16	0.22 ± 0.11	0.02 ± 0.06	-0.12 ± 0.06	-0.17 ± 0.05
17.	Older successional	0.03 ± 0.10	-0.01 ± 0.05	0.42 ± 0.12	0.06 ± 0.35	-0.14 ± 0.07

Table 62. SMR analysis of the abundance and distribution of *P. maniculatus* in 1979. (See Table 18 for explanation of variable names. Multiple r-square = 0.4816; standard error of estimate = 0.0564; df = 7,139; F-ratio = 18.44; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.067				
Jack pine understory	1	0.035	0.004	0.2995	0.2995	***
Aspen understory	2	0.016	0.005	0.3734	0.0740	***
Balsam poplar understory	3	-0.018	0.005	0.4078	0.0344	***
Raspberry shrub	4	-0.011	0.005	0.4266	0.0188	*
Grass/sedge cover	5	-0.013	0.005	0.4449	0.0184	*
Successional cover	6	-0.013	0.005	0.4665	0.0215	*
Equisetum cover	7	-0.009	0.004	0.4816	0.0151	*

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 63. Mean factor scores for study areas included in the five-study area factor analysis in 1979. (Mean factor scores and 1 S.E. are indicated for each factor based on the factor scores for each of the 30 samples on each area. The Willow, Black spruce, and Tamarack study areas were not included in the analysis because of the extremely low numbers of animals captured in these areas.)

Factor	Jack pine	Aspen	Balsam poplar	Poplar Creek cutline	Thickwood cutline
	Study Areas				
1. Aspen understory	1.71 ± 0.17	-0.39 ± 0.07	-0.27 ± 0.04	-0.41 ± 0.04	-0.64 ± 0.04
2. Balsam poplar understory	-0.32 ± 0.08	-0.13 ± 0.05	1.97 ± 0.14	-0.34 ± 0.07	-0.47 ± 0.09
3. Jack pine understory	-0.26 ± 0.08	1.87 ± 0.21	-0.34 ± 0.05	-0.43 ± 0.06	-0.50 ± 0.07
4. Dense vertical cover	-0.23 ± 0.12	-0.11 ± 0.12	0.39 ± 0.14	-0.17 ± 0.16	-0.88 ± 0.08
5. Successional cover	-0.41 ± 0.07	-0.16 ± 0.04	-0.26 ± 0.05	1.39 ± 0.24	-0.65 ± 0.07
6. Tamarack forest	-0.12 ± 0.09	0.47 ± 0.50	0.01 ± 0.05	-0.10 ± 0.05	-0.11 ± 0.05
7. Rose understory	0.71 ± 0.22	-0.30 ± 0.08	0.07 ± 0.20	-0.11 ± 0.18	0.17 ± 0.22
8. Raspberry shrub	-0.24 ± 0.10	-0.20 ± 0.07	0.30 ± 0.31	-0.05 ± 0.17	0.50 ± 0.17
9. *Viburnum* shrub	0.20 ± 0.32	-0.10 ± 0.05	-0.05 ± 0.22	-0.19 ± 0.10	-0.29 ± 0.06
10. Dwarf birch shrub	-0.03 ± 0.07	0.59 ± 0.54	-0.12 ± 0.04	-0.05 ± 0.03	-0.03 ± 0.03
11. Grass/sedge cover	0.02 ± 0.10	-0.11 ± 0.07	-0.14 ± 0.12	0.84 ± 0.30	0.26 ± 0.10
12. Dogwood shrub	0.05 ± 0.08	-0.17 ± 0.08	0.32 ± 0.32	-0.12 ± 0.09	-0.06 ± 0.09
13. Fireweed cover	-0.39 ± 0.13	-0.05 ± 0.09	-0.36 ± 0.06	-0.37 ± 0.12	0.61 ± 0.23
14. Black spruce ground cover	0.55 ± 0.23	0.88 ± 0.46	-0.11 ± 0.03	-0.09 ± 0.04	-0.24 ± 0.03
15. *Equisetum* cover	0.01 ± 0.12	-0.28 ± 0.12	0.07 ± 0.15	-0.04 ± 0.17	0.83 ± 0.30
16. Black spruce - white spruce transition	0.60 ± 0.36	-0.14 ± 0.37	-0.04 ± 0.06	-0.05 ± 0.06	-0.09 ± 0.06
17. Older successional	-0.14 ± 0.10	-0.23 ± 0.08	-0.34 ± 0.13	0.38 ± 0.36	-0.03 ± 0.10

Table 64. Forced SMR analysis of the abundance and distribution of *P. maniculatus* in 1979. (All predictor variables found to be significant in 1978 were included in this reanalysis of the 1979 data. See Table 18 for explanation of variable names. Multiple r-square = 0.5252; standard error of the regression = 0.0546; df = 7,142; F-ratio = 22.44; $P < 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.067				
Balsam poplar understory	1	0.049	0.005	0.0218	0.0218	NS
Jack pine understory	2	-0.014	0.004	0.0867	0.0648	***
Successional cover	3	0.018	0.005	0.1056	0.0189	*
Aspen understory	4	0.049	0.005	0.4573	0.3517	***
Equisetum cover	5	-0.006	0.004	0.4647	0.0074	NS
Grass/sedge cover	6	0.019	0.005	0.5221	0.0573	***
Dense vertical cover	7	0.006	0.006	0.5252	0.0032	NS

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

11.4 SNOWSHOE HARES

11.4.1 Principal Components Analysis of Vegetation on the Snowshoe Hare Study Areas

A factor (principal components) analysis was used to reduce a large number of habitat variables to a smaller number of independent variables. Based on the results of the vegetation sampling program in 1979, a total of 43 different habitat variables [one estimate of the cumulative density of the forest canopy, estimates of the percent coverage of 17 ground cover species (or species groups), and the relative abundance of 25 species of trees and shrubs] were recorded in the four study areas during the vegetation sampling program in 1979. Relationships between species or species groups occurring in less than 10 samples (on all four grids combined) and habitat structure were unlikely to be detectable, even if real, and consequently were not included in further analyses. This reduced the number of variables considered to 28. For input to the factor analysis, the three most dominant tree and shrub species, respectively, in each sample were ranked on a scale of 1 to 9, based on the abundance of a species in the sampling plot and the number of other tree and shrub species present. Ground cover species were ranked according to the Braun-Blanquet cover scale (Kershaw 1966).

A factor analysis was performed on the vegetation data using the BMDP4M computer program (Dixon and Brown 1979) using a standard method--a principal components analysis followed by Varimax (orthogonal) rotation of those principal components with eigenvalues exceeding 1.0. The factor analysis of vegetation on the four snowshoe hare study areas transformed the 28 habitat variables into a series of nine uncorrelated factors. Rotated factor loadings are summarized in Table 68. Interpretations of each of the nine factors are summarized in Table 25.

Table 65. Breeding activity of mature snowshoe hares. (Numbers of mature snowshoe hares and the proportion in breeding condition are indicated for each trapping period during the summer periods of 1978 and 1979.)

	Jack pine				Aspen				Balsam poplar				Black spruce			
	Males		Females		Males		Females		Males		Females		Males		Females	
Date[a]	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N	Prop.	N
1978																
1 July	0.00	1	-	0	-	0	0.00	1	0.00	3	0.00	3	0.20	10	0.25	4
19 July	-	0	-	0	-	0	-	0	0.25	4	0.00	1	0.22	9	0.27	11
1 August	0.50	2	0.50	2	0.50	2	-	0	0.75	4	0.00	3	0.20	10	0.23	13
16 August	0.50	2	0.00	1	0.33	3	-	0	0.33	6	0.67	3	0.33	9	0.13	15
27 August	0.33	3	0.50	2	0.25	8	0.50	2	0.20	5	0.00	3	0.18	17	0.00	15
15 September	0.00	4	0.33	3	0.00	6	0.00	1	0.00	4	0.00	5	0.08	12	0.00	15
1979																
16 May	0.25	4	0.86	7	0.33	3	0.83	6	0.50	8	0.50	4	0.43	14	0.64	14
8 June	0.50	2	1.00	3	0.67	3	0.20	5	0.80	5	0.83	6	0.60	15	1.00	10
24 June	1.00	3	0.50	2	1.00	2	0.00	2	0.40	5	0.33	6	0.36	14	0.71	7
18 July	0.43	7	0.50	4	-	0	0.33	3	0.13	8	0.36	11	0.55	11	0.43	14
10 August	0.33	3	0.57	7	0.67	3	0.00	3	0.13	8	0.43	7	0.27	11	0.10	10
31 August	0.33	3	1.00	1	0.00	6	0.00	7	0.20	5	0.00	3	0.13	15	0.25	8
20 September	0.25	4	0.67	3	0.20	5	0.00	8	0.00	10	0.60	5	0.00	15	0.67	9

[a] Dates shown are the mid-point of each trapping period.

Table 66. Juvenile recruitment rates of *L. americanus*. (Rates shown are expressed as the number of new juvenile snowshoe hares captured per breeding adult female during each summer trapping period. Numbers of adult females are also indicated.)

		Jack pine		Aspen		Balsam poplar		Black spruce	
	Date[a]	Rate	N	Rate	N	Rate	N	Rate	N
1978	1 July	1.00	1	-	0	1.67	3	1.30	10
	19 July	-	0	-	0	0.00	4	0.88	9
	1 August	0.00	2	0.00	2	0.25	4	0.50	10
	16 August	0.00	2	0.67	3	0.00	6	0.56	9
	27 August	0.33	3	0.50	8	0.60	5	0.41	17
	15 September	0.00	4	0.00	6	0.00	4	0.17	12
1979	16 May	0.00	4	0.00	3	0.00	8	0.00	14
	8 June	0.00	2	1.33	3	0.40	5	0.20	15
	24 June	0.33	3	0.50	2	1.20	5	0.57	14
	18 July	0.71	7	-	0	1.00	8	0.63	11
	10 August	1.00	3	1.00	3	0.88	8	0.82	11
	31 August	0.33	3	1.67	6	0.40	5	0.60	15
	20 September	0.00	4	0.20	5	-	0	0.00	15

[a] Dates shown are the mid-point of each trapping period.

Table 67. Mean body weights of snowshoe hares. (Mean body weight, 1 S.E. of the mean and sample sizes of juvenile, sub-adult, and adult adult snowshoe hares during each trapping period are indicated.)

Age Class		Date[a]	Jack pine			Aspen			Balsam poplar			Black spruce		
			Wt.	1 S.E.	N	Wt.	1 S.E.	N	Wt.	1 S.E.	N	Wt.	1 S.E.	N
Juveniles	1978	1 July	195	-	1	785	-	1	772	15	5	683	43	12
		19 July	-	-	0	-	-	0	963	13	2	665	76	13
		1 August	-	-	0	-	-	0	525	-	1	710	46	12
		16 August	-	-	0	398	88	2	-	-	0	593	86	8
		27 August	530	-	1	562	71	6	813	104	3	694	67	12
		15 September	-	-	0	845	28	4	855	-	1	655	54	9
		25 September	880	-	1	880	14	4	765	125	2	773	40	9
		15 October	-	-	0	-	-	0	939	14	5	913	25	7
		27 October	-	-	0	-	-	0	938	6	4	930	18	5
		9 November	-	-	0	-	-	0	980	-	1	923	37	4
	1979	3 March	-	-	0	-	-	0	-	-	0	-	-	0
		16 May	-	-	0	-	-	0	-	-	0	-	-	0
		8 June	975	-	1	255	12	4	315	55	2	456	344	3
		24 June	501	137	5	447	52	3	481	13	7	253	18	9
		18 July	658	64	5	865	35	2	699	70	10	413	44	10
		10 August	750	200	2	567	44	3	684	79	7	525	51	12
		31 August	-	-	0	439	67	10	898	23	2	709	65	14
		20 September	945	-	1	608	17	6	800	-	1	875	78	3
		13 October	-	-	0	835	65	2	-	-	0	940	-	1
		9 November	-	-	0	-	-	0	-	-	0	-	-	0
		31 November	-	-	0	-	-	0	-	-	0	-	-	0
	1980	26 January	-	-	0	-	-	0	-	-	0	-	-	0
Sub-adults	1978	1 July	-	-	0	-	-	0	1000	-	1	1000	-	1
		19 July	-	-	0	-	-	0	-	-	0	1075	35	4
		1 August	1050	-	1	1088	63	2	1075	27	4	1099	33	7
		16 August	-	-	0	-	-	0	1260	70	3	1155	41	11
		27 August	1405	-	1	1350	80	2	1283	50	4	1167	29	15
		15 September	1440	-	1	1298	208	2	1270	86	5	1276	33	15
		25 September	1630	-	1	1268	66	5	1310	52	5	1360	30	18
		15 October	-	-	0	1223	54	6	1312	36	9	1361	32	17
		27 October	-	-	0	1173	43	6	1307	29	8	1335	33	20
		9 November	-	-	0	-	-	0	1270	49	5	1365	33	15
	1979	3 March	-	-	0	1363	12	3	1233	24	9	1339	32	9
		16 May	-	-	0	1108	71	3	-	-	0	1238	103	4
		8 June	-	-	0	1210	-	1	1405	-	1	1187	115	3
		24 June	-	-	0	-	-	0	-	-	0	1315	-	1
		18 July	-	-	0	-	-	0	1293	85	4	1320	80	2
		10 August	-	-	0	-	-	0	1224	69	5	1340	-	1
		31 August	-	-	0	1245	145	2	1281	53	4	1050	-	1
		20 September	1108	63	2	1307	98	3	1381	74	8	1224	40	11
		13 October	1195	-	1	-	-	0	1413	120	3	1263	35	17
		9 November	1180	49	5	1250	-	1	1435	29	19	1283	38	8
		31 November	1197	47	3	1277	39	3	1438	26	12	1310	28	13
	1980	26 January	-	-	0	1228	29	6	1482	50	5	1317	50	7

continued...

Table 67. Concluded.

Age Class		Date[a]	Jack pine			Aspen			Balsam poplar			Black spruce		
			Wt.	1 S.E.	N	Wt.	1 S.E.	N	Wt.	1 S.E.	N	Wt.	1 S.E.	N
Adults	1978	1 July	-	-	0	-	-	0	-	-	0	1000	-	1
		19 July	-	-	0	-	-	0	1708	109	3	1558	252	3
		1 August	1350	156	3	-	-	0	1588	38	2	1413	32	4
		16 August	1353	111	3	1535	-	1	1412	28	6	1513	115	5
		27 August	1430	58	3	1533	23	2	1550	-	1	1536	69	5
		15 September	1425	33	6	1490	-	1	1327	13	3	1483	30	3
		25 September	1408	57	7	-	-	0	1353	13	4	1515	48	4
		15 October	1481	57	7	-	-	0	1415	63	4	1457	44	3
		27 October	1370	170	2	-	-	0	1390	150	2	1455	25	2
		9 November	1456	44	3	-	-	0	1440	100	2	-	-	0
	1979	3 March	1490	-	1	-	-	0	1381	21	9	1359	65	4
		16 May	1375	59	11	1379	41	6	1435	52	12	1260	26	24
		8 June	1376	70	5	1525	168	3	1507	88	7	1322	36	19
		24 June	1566	166	4	1790	-	1	1588	186	4	1448	54	11
		18 July	1535	93	6	1400	-	1	1496	49	5	1334	74	13
		10 August	1390	79	5	1537	48	3	1630	117	3	1406	22	8
		31 August	1578	213	2	1600	-	1	1450	100	2	1463	89	8
		20 September	1550	44	5	1665	18	4	1520	49	6	1516	36	10
		13 October	1608	81	6	-	-	0	1518	44	4	1536	42	11
		9 November	1582	50	8	-	-	0	1604	32	9	1491	35	9
		31 November	1516	129	5	1680	-	1	1624	40	9	1452	37	10
	1980	26 January	1534	85	9	1541	68	4	1469	38	11	1440	34	10

[a] Dates shown are the mid-points of each trapping period.

Table 68. Factor loadings for the four study area factor analysis. [Only the correlations between the original variables and the 9 factors whose absolute values were ≥ 0.250 are shown. Only factors with VP's (total variance in vegetation structure that was explained by the factor) that exceeded 1.5 were included in the SMR. The variable prefixes PR and GC refer to dominance in the forest canopy and ground cover respectively.]

Variable	Factor								
	1	2	3	4	5	6	7	8	9
PR - *Alnus* spp.	0.791							0.335	
PR - *P. balsamifera*	0.740							0.287	
Density of Canopy	0.728								
PR - *C. stolonifera*	0.728								0.300
GC - *Equisetum* spp.	0.684								
PR - *Viburnum* spp.	0.558								
PR - *P. tremuloides*		0.736							
GC - *A. uva-ursi*		0.734							
PR - *A. alnifolia*		0.712							
PR - *P. mariana*	-0.339	-0.583	-0.417						
GC - Moss	-0.337	-0.507			-0.423			-0.311	
PR - *P. glauca*			0.758			0.358			
GC - *C. canadensis*			0.673						
Absence of ground cover				0.872					
Absence of tree cover				0.871					
Absence of shrub cover				0.261	0.767				
GC - *Cladonia/Cladina* spp.	-0.267				0.694		0.290		
PR - *B. glandulosa*						0.743			
GC - *V. caespitosum*							0.829		
GC - *M. paniculata*								0.734	
PR - *B. papyrifera*									0.923
PR - *L. laricina*	-0.360	-0.275	-0.286		-0.300			0.253	
GC - *V. vitis-idaea*	-0.280	-0.260			0.289	-0.471			
GC - *V. uliginosum*		0.446					-0.420		
PR - *Salix* spp.	-0.379	-0.485	-0.257		-0.449				
GC - *L. groenlandicum*	-0.258	-0.410				0.379			
PR - *S. canadensis*		0.362	0.456				-0.254		
PR - *Rosa* spp.		0.254	0.380					0.272	
VP	4.120	3.241	1.937	1.824	1.821	1.366	1.292	1.259	1.129

Table 69. SMR analysis of the abundance and distribution of *L. americanus* during the spring and summer of 1978. (See Table 25 for explanation of variable names. Multiple r-square = 0.3359; standard error of estimate = 0.0271; df = 5,310; F-ratio = 31.36; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.028				
+Aspen/-Black spruce forest	1	-0.005	0.002	0.1661	0.1661	***
+White spruce/-Black spruce forest	2	-0.013	0.002	0.2463	0.0801	***
Jack pine understory	3	-0.009	0.002	0.2945	0.0483	***
Shrub birch-white spruce transition	4	-0.007	0.002	0.3174	0.228	***
Balsam poplar forest	5	-0.005	0.002	0.3359	0.0186	***

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 70. Mean factor scores for the four snowshoe hare study areas. (Mean factor scores and 1 S.E. are indicated for each factor based on the factor scores for each of the 30 samples on each plot.)

Factor	Study Areas			
	Jack pine	Aspen	Balsam Poplar	Black spruce
1. Balsam poplar forest	-0.48 ± 0.03	-0.30 ± 0.04	1.53 ± 0.09	-0.68 ± 0.05
2. +Aspen/-Black spruce forest	0.20 ± 0.11	0.96 ± 0.10	-0.16 ± 0.03	-1.01 ± 0.03
3. +White spruce/-Black spruce forest	0.24 ± 0.10	0.69 ± 0.13	-0.22 ± 0.07	-0.72 ± 0.05
4. Open Habitat	-0.12 ± 0.06	-0.05 ± 0.02	0.52 ± 0.21	-0.32 ± 0.02
5. Jack pine understory	0.60 ± 0.15	-0.36 ± 0.04	-0.05 ± 0.03	-0.19 ± 0.14
6. Shrub birch-white spruce transition	0.57 ± 0.15	-0.30 ± 0.08	-0.01 ± 0.04	-0.26 ± 0.12
7. *V. caespitosum*	0.54 ± 0.16	-0.27 ± 0.10	-0.04 ± 0.03	-0.23 ± 0.09
8. Bluebell Cover	0.07 ± 0.07	-0.27 ± 0.06	0.45 ± 0.17	-0.23 ± 0.10
9. Paper Birch	0.01 ± 0.04	-0.04 ± 0.13	0.13 ± 0.23	-0.09 ± 0.04

Table 71. SMR analysis of the abundance and distribution of *L. americanus* during the spring and summer of 1979. (See Table 25 for explanation of variable names. Multiple r-square = 0.2811; standard error of estimate = 0.0341; df = 3,312; F-ratio = 40.66; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P[a]
Constant		0.038				
+Aspen/-Black spruce forest	1	-0.018	0.002	0.2032	0.2032	***
+White spruce/-Black spruce forest	2	-0.009	0.002	0.2523	0.0492	***
Jack pine understory	3	-0.007	0.002	0.2811	0.0287	***

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 72. SMR analysis of the abundance and distribution of *L. americanus* during the winter of 1978-1979. (See Table 25 for explanation of variable names. Multiple r-square = 0.1491; standard error of estimate = 0.0287; df = 5,310; F-ratio = 10.86; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant		0.014				
+Aspen/-Black spruce forest	1	-0.005	0.002	0.0602	0.0602	***
Jack pine understory	2	-0.008	0.002	0.0875	0.0273	***
Balsam poplar forest	3	-0.005	0.002	0.1125	0.0250	***
+White spruce/-Black spruce forest	4	-0.005	0.002	0.1365	0.0240	***
Shrub birch-white spruce transition	5	-0.003	0.002	0.1491	0.0126	***

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

Table 73. SMR analysis of the abundance and distribution of *L. americanus* during the winter of 1979-1980. (See Table 25 for explanation of variable names. Multiple r-square = 0.1009; standard error of estimate = 0.0015; df = 2,313; F-ratio = 17.57; $P \leq 0.001$.)

Variable Name	Step at which Factor Entered Equation	Regression Coefficient at Last Step	S.E. of Regression Coefficient at Last Step	R^2 at Each Step	Increase in R^2 Attributable to Factor	P^a
Constant	0.001					
+Aspen/-Black spruce forest	-0.001	-0.296	0.000	0.0873	0.0873	***
Jack pine understory	-0.001	-0.117	0.-00	0.1009	0.0136	***

[a] Two-sided significance levels: * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$.

12. LIST OF AOSERP RESEARCH REPORTS

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2.	AF 4.1.1	Walleye and Goldeye Fisheries Investigations in the Peace-Athabasca Delta--1975
3.	HE 1.1.1	Structure of a Traditional Baseline Data System
4.	VE 2.2	A Preliminary Vegetation Survey of the Alberta Oil Sands Environmental Research Program Study Area
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14.		
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